European Journal of Taxonomy 833: 60–96
https://doi.org/10.5852/ejt.2022.833.1887
ISSN 2118-9773
www.europeanjournaloftaxonomy.eu
2022 · Martin D. *et al.*



**Research article**

urn:lsid:zoobank.org:pub:F2C142A4-94C0-4D5E-86AD-925F23103A95

# Taxonomic implications of describing a new species of *Loimia* (Annelida, Terebellidae) with two size-dependent morphotypes

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**Abstract.** We describe *Loimia davidi* sp. nov. (Annelida, Terebellidae) from São Miguel Island (Açores). It resembles *Loimia gigantea* (Montagu, 1819) (English Channel) in having very large adults, the ventral shield shape and the types of capillary notochaetae (three), while differing in shape and colour of the lateral lappets, branchiae length, the arrangement of segments, ventral shields, uncini and pygidial papillae. Large (> 30 cm long) and small (≈ 5 cm long) specimens of *L. davidi* sp. nov. show typically interspecific morphological differences while clustering in a single entity after species delimitation analyses of a cytochrome c oxidase I fragment. Therefore, we consider them to belong to a single species and discuss the taxonomic implications of size-dependent morphological differences. Within *Loimia*, we (1) suggest that large specimens may have been scarcely reported due to their rarity and collecting difficulty, while small specimens may have been reported either as 'sp.' or as the 'cosmopolitan' *Loimia medusa* (Savigny, 1822), (2) evaluate the size-related morphological disparity in all described species using a hypervolume analysis, (3) identify possible similar size-dependency in previously described species, (4) summarise the morphological information of all known species of *Loimia*; and (5) discuss the four species reported in Europe.

**Keywords.** *Loimia*, Açores Archipelago, North East Atlantic, intraspecific morphological variability, intraspecific genetic distance, integrative taxonomy.

Martin D., Capa M., Martínez A. & Costa A.C. 2022. Taxonomic implications of describing a new species of *Loimia* (Annelida, Terebellidae) with two size-dependent morphotypes. *European Journal of Taxonomy* 833: 60–96. https://doi.org/10.5852/ejt.2022.833.1887

## Introduction

Benthic communities play a fundamental role in marine coastal areas, where they influence ecosystem services such as nutrient and sediment transport as well as primary and secondary productivity (Levin *et al.* 2001; Austen *et al.* 2002). Yet, many species integrated in these communities remain undescribed, hindering our understanding of the eco-evolutionary processes affecting shallow-water marine ecosystems and their resilience to disturbances (Sánchez-Quiles & Tovar-Sánchez 2015). This holds true even for the comparatively well-studied European waters, where many new species are still being described every year. This taxonomic gap is often justified through the so-called taxonomic impediment (Wheeler *et al.* 2004), since many of these undescribed species are microscopic members of the meiobenthos (Brannock *et al.* 2014; Worsaae *et al.* 2015), or cryptic lineages demanding time-consuming integrative taxonomic methods to be unravelled (e.g., Appeltans *et al.* 2012; Nygren *et al.* 2018; Grosse *et al.* 2020, 2021; Parapar *et al.* 2020). However, several recent findings of conspicuous and morphologically distinct organisms have also been attributed to undescribed species. Indeed, several annelids, including large species of Chaetopteridae Audouin & Milne Edwards, 1833 or Terebellidae Johnston, 1846, have recently been described based on morphological analyses, sometimes even from the front garden of core European marine facilities (Martin *et al.* 2008; Lavesque *et al.* 2017).

The species of *Loimia* Malmgren, 1866 (Annelida Lamarck, 1809, Terebellidae) deserve a special mention amongst those conspicuous – yet overlooked – components of the infaunal coastal communities (Hutchings *et al.* 2020). One-third of the 31 currently accepted species have been described within the last decade (Read & Fauchald 2021), mostly from tropical and subtropical areas (e.g., Carrerette & Nogueira 2015; Nogueira *et al.* 2015). Four species are known from European Atlantic temperate waters, with three of them having their type locality in the area. The first is the type species of the genus, *Loimia medusa* (Savigny, 1822). This species was originally described from the Gulf of Suez by Savigny (1822) and subsequently reported from the Mediterranean Sea and the Atlantic Ocean, from Northern Africa to Norway (Fauvel 1936; Gil 2011; Lavesque *et al.* 2021). It was considered to be absent in the British islands and nearby waters, with the records in this area being successively attributed to two different species (McIntosh 1915, 1922). However, many of these records were based on limited or even incomplete material. Thus, new collections seem crucial to allow a resolution of this question. Indeed, *L. medusa* appears to be restricted to the coasts surrounding the Arabian Peninsula, emphasizing the need for a revision of all European records of the genus (Hutchings & Glasby 1995).

The second species, *Loimia ramzega* Lavesque, Bonifácio, Londoño-Mesa, Le Garrec & Grall, 2017, was discovered on the western coasts of France. It was reported from a few localities near the Roscoff, Brest, and the Arcachon Marine Stations (Lavesque *et al.* 2017). The description of such a large species (it reaches a length of 65 cm) in a historically well-studied area was regarded as surprising by Lavesque *et al.* (2017), who suggested that the species might have been recently introduced in European waters, remained hidden among the numerous existing reports of non-identified specimens of *Loimia* of the area or was confused with *L. medusa*. Nevertheless, the presence of *Loimia* in the western English Channel has been well known for more than 150 years, with a species being reported by McIntosh (1869) (as *Terebella medusa*). Moreover, several species were officially described and named in the region. In fact, the presence of *Loimia* on both sides of the English Channel can be traced back to at least 1863, when the larval and post-larval development of local populations was described in detail in at least two papers (Claparède 1863; Wilson 1928).

The third species, *Loimia montagui*, was described by McIntosh (1922) from the coasts of Devon and neighbouring areas (including the Plymouth region) in the western English Channel, just along the opposite coast facing the type locality of *L. ramzega*. This species has been traditionally overlooked due to a poorly understood case of homonymy involving two other species (e.g., Lavesque *et al.* 2017,

2021). However, this pretended homonymy does not exist. Thus, the name would be valid had it not been for the fact that it is itself a junior synonym of an even older species in the region.

Last but not least, there is a fourth species from the Devon coasts of the English Channel, also overlooked in previous works (e.g., Lavesque *et al.* 2017, 2021). This is a large-sized species described two centuries ago as *Terebella gigantea* by Montagu (1819), recombined as *Loimia gigantea* by McIntosh (1915) and later renamed as *L. montagui* by McIntosh (1922), due to an identification error introduced by Grube (1870) (see Discussion). This fourth species is here considered to represent a senior synonym of both *L. montagui* and *L. ramzega*, besides comprising no less than the European records of *L. medusa* from the English Channel and nearby waters.

We here provide new insights into the systematics of *Loimia* based on freshly collected material from the Açores Archipelago, where the genus had previously not been recorded (Cordeiro *et al.* 2019; Freitas *et al.* 2019). We unequivocally attribute these specimens to *Loimia* (sensu Carrerette & Nogueira 2015; Nogueira *et al.* 2015), as they (1) lack a proboscis, and present (2) arborescent branchiae, (3) 17 thoracic segments with smooth capillary chaetae and (4) double rows of pectinate uncini arranged back-to-back from segment 11. We also find them nested within a clade with other species of *Loimia* after analyses of mitochondrial cytochrome C oxidase I (*cox1*) sequences. Indeed, morphological and molecular evidence indicates that the Azorean specimens belong to a new species, whose formal description is the first aim of this study. Our specimens, however, show a broad morphological variability related to their considerable differences in body size, thus questioning the limits of the intraspecific variability of the other species of *Loimia*. Therefore, our second aim is to review the morphological characters used to diagnose all the other nominal species in the genus. With this purpose, we focus on the possible existence of a size-related morphological variability by calculating the relative position of the small and large Azorean specimens in relation to the morpho-space of all the species of *Loimia* using n-dimensional hypervolumes, while providing a semi-qualitative account for the morphological variability of the group.

## Material and methods

### Sampling and morphological observations

Sampling was performed by SCUBA diving within the frame of the Açores Workshop on Polychaete Taxonomy (10–12 July 2017), organised by the Research Centre for Biodiversity and Genetic Resources (InBIO/CIBIO, Universidade dos Açores) at São Miguel Island (Açores, Portugal). Specimens of *Loimia* were collected at Rostro de Cão, near Ponta Delgada, in an area with coarse sand patches accumulated among large boulders at a depth of 8 m. Divers manually dug the animals out of the sand and immediately transferred them to hermetic plastic bags filled with seawater. In the laboratory, the largest individual was filmed and photographed with an iPhone 8 Plus prior to preservation. A mid-abdominal fragment was then dissected apart and preserved in 96% ethanol for DNA extraction. The two remaining body fragments – corresponding to the thorax with the most anterior abdominal segments, and the posterior abdominal region with the pygidium – were fixed in a 4% dilution of formalin in seawater for 24 hours, rinsed, and transferred to 70% ethanol. Among the remaining individuals, nine were directly preserved in 96% ethanol and the other nine were fixed in a 4% formalin solution in seawater before being permanently transferred to 70% ethanol.

Light micrographs of fixed specimens were taken with a CMEX 5 digital camera connected to a ZEISS Stemi CS–2000–C stereo microscope and with a SP100 KAF1400 digital camera connected to a Zeiss Axioplan compound microscope. The morphological features are described following the terminology established by Nogueira *et al.* (2010).

The specimens of the new species are deposited at the Collections of the Centre d'Estudis Avançats de Blanes (CEAB) and the Museo Nacional de Ciencias Naturales of Madrid (MNCN). Additionally, we

examined two specimens of *L. gigantea* (as *L. ramzega*) loaned from the collections of the Arcachon Marine Station, France (ARC).

**DNA isolation, amplification, and sequencing**

Genomic DNA was extracted from the mid-abdominal fragment of the largest specimen and from two of the small individuals. Several abdominal parapodia were dissected and placed in tubes containing 50 µL of QuickExtract (Epicentre), incubated at 65°C for 60 minutes, and centrifuged at 95°C for 3 minutes in a thermos-shaker at 300 rpm. Then, each extraction was diluted by adding 200 µL of elution buffer.

*Cox1* fragments were amplified using jgLCO/jgHCO (Geller *et al.* 2013) or ArR5/ArF5 primers (Gibson *et al.* 2014). PCR mixtures contained 1 µl of each primer (10 ng/µl), 7.5 µL of MyTaq Red Mix (Bioline), 1 µl of DNA template (~5-20 ng/µl), and 4.5 µl of water dd$H_2O$. The PCR thermal cycling profile included an initial denaturation at 96°C for 3 minutes, followed by 34 cycles with three steps: (1) denaturation at 95°C for 60 seconds, (2) annealing at 48°C for 60 seconds, and (3) extension at 72°C for 60 seconds. Each reaction was finalized with an additional 6-min extension step at 72°C. The products of successful amplifications were purified using the ExoSAP-IT PCR product cleanup (USB Corporation) and bidirectionally sequenced at Eurofins (Germany) using a BigDye Terminator v634 sequencer (Applied Biosystems). Chromatograms and contigs were visually inspected, and primer sequences trimmed using Geneious Prime 2020.2. Subsequently, all contigs were blasted in NCBI GenBank for possible contamination and translated into amino acids to confirm the absence of stop codons, which might indicate the amplification of pseudogenes.

Despite the many attempts using different PCR mixes and thermal cycling profiles, the amplification of the mitochondrial 16SrRNA fragments using primers 16SArL/16SBrH (Palumbi 1996) remained unsuccessful. All the sequences obtained in this study have been deposited in GenBank (http://www.ncbi.nlm.nih.gov/genbank/) (Table 1).

**Molecular analyses**

Our molecular dataset included all the *cox1* sequences available in GenBank for *Loimia*, as well as the three newly obtained sequences from the Açores (Table 1). One species of *Lanice* Malmgren, 1866 was used as an outgroup (McHugh 1995; Garraffoni & Lana 2008, 2010; Nogueira *et al.* 2013; Stiller *et al.* 2020). Alignments were performed in the program MAFFT (Katoh *et al.* 2002; Katoh & Standley 2013) using the iterative refinement method L-INS-i, and default gap open and extension penalization parameters. Alignment was trimmed to 402 base pairs after the length of our newly produced sequences. Maximum likelihood (ML) analyses were implemented in IQ-TREE (Nguyen *et al.* 2015; Trifinopoulos *et al.* 2016), which also selected the best fitting evolutionary model based on the Bayesian Information Criterion (BIC) (TVM+F+I+G4). Nodal support values were estimated based on 1000 bootstrap ultrafast pseudoreplicates (Hoang *et al.* 2018).

To delimit the species of *Loimia* and to assess if our specimens corresponded to one or two genetic lineages compatible with the evolutionary species concept (understood as evolutionary independent lineages), both a Poison Tree (PTP, Zhang *et al.* 2013) and a multi-rate Poison Tree (mPTP, Kapli *et al.* 2017) process model were implemented on the *cox1* ML tree in the mPTP webserver (https://www.h-its.org/software/mptp-web-server/). The *p* value of the PTP model was 0.01. The sequence of *Lanice* included as an outgroup was removed from both analyses.

The evolutionary divergences over sequence pairs between and within species of *Loimia*, according to the PTP output, were calculated using MEGA X (Kumar *et al.* 2018) after removing all ambiguous

**Table 1** (continued on next page). GenBank accession codes and voucher references for the sequences of the species of *Loimia* Malmgren, 19866 used in the phylogenetic analysis, including localities, geographical coordinates and region (when available), and associated literature.

| Species | Locality | Latitude and longitude | Region | Voucher | Accesion number | Reference |
|---|---|---|---|---|---|---|
| *L. arborea* | Queen Charlotte Sound, British Columbia, Canada | – | NE Pacific | – | HM473449 | Carr *et al.* (2011) |
| *L. arborea* | Off Shangai, China | 30°59′28.6″ N 122°20′39.7″ E | NW Pacific | MBM286581 | MN133250 | Wang *et al.* (2020) |
| *L. arborea* | Yellow Sea, China | 36°59′45.6″ N 122°59′31.2″ E | NW Pacific | MBM286582 | MN133249 | Wang *et al.* (2020) |
| *L. bandera* | Taiwan Strait, China | 25°50′26.9″ N 120°14′50.3″ E | NW Pacific | MBM286584 | MN133252 | Wang *et al.* (2020) |
| *L. bandera* | Taiwan Strait, China | 25°50′26.9″ N 120°14′50.3″ E | NW Pacific | MBM286583 | MN133251 | Wang *et al.* (2020) |
| *L. borealis* | Shouguang City, Shandong Peninsula, China | 37°16′34.0″ N 119°02′19.4″ E | NW Pacific | MBM286591 | MN133237 | Wang *et al.* (2020) |
| *L. borealis* | Shouguang City, Shandong Peninsula, China | 37°16′34.0″ N 119°02′19.4″ E | NW Pacific | MBM286593 | MN133238 | Wang *et al.* (2020) |
| *L. borealis* | Shouguang City, Shandong Peninsula, China | 37°16′34.0″ N 119°02′19.4″ E | NW Pacific | MBM286592 | MN133239 | Wang *et al.* (2020) |
| *L. borealis* | Shouguang City, Shandong Peninsula, China | 37°16′34.0″ N 119°02′19.4″ E | NW Pacific | MBM286585 | MN133240 | Wang *et al.* (2020) |
| *L. davidi* sp. nov. (large) | Ilhéu de São Roque, São Miguel Island, Açores | 37°44′37.0″ N 25°38′17.0″ W | NE Atlantic | CEAB A.P. 935C | MZ382866 | present study |
| *L. davidi* sp. nov. (small) | Ilhéu de São Roque, São Miguel Island, Açores | 37°44′37.0″ N 25°38′17.0″ W | NE Atlantic | CEAB A.P. 935C | MZ382867 | present study |
| *L. davidi* sp. nov. (small) | Ilhéu de São Roque, São Miguel Island, Açores | 37°44′37.0″ N 25°38′17.0″ W | NE Atlantic | CEAB A.P. 935C | MZ382868 | present study |
| *L. gigantea* | Landeda beach, Brittany, English Channel | 48°37′37.2″ N 4°34′08.5″ W | NE Atlantic | MNHN–IA–TYP E 1788 | KY555063 | Lavesque *et al.* (2017) |
| *L. gigantea* | Landeda beach, Brittany, English Channel | 48°37′37.2″ N 4°34′08.5″ W | NE Atlantic | MNHN–IA–TYP E 1789 | KY555062 | Lavesque *et al.* (2017) |
| *L. gigantea* | Landeda beach, Brittany, English Channel | 48°37′37.2″ N 4°34′08.5″ W | NE Atlantic | MNHN–IA–TYP E 1790 | KY555061 | Lavesque *et al.* (2017) |
| *L. ingens* | Phuket, Thailand, Andaman Sea | – | E Indian Ocean | – | AF342685 | Colgan *et al.* (2001) |

**Table 1** (continued). GenBank accession codes and voucher references for the sequences of the species of *Loimia* Malmgren, 1866 used in the phylogenetic analysis, including localities, geographical coordinates and region (when available), and associated literature.

| Species | Locality | Latitude and longitude | Region | Voucher | Accesion number | Reference |
|---|---|---|---|---|---|---|
| *L. ingens* | Linqiangshidao Island, China | 21°04′46.5″ N 109°06′20.0″ E | NW Pacific | MBM286604 | MN133248 | Wang *et al.* (2020) |
| *L. ingens* | Weizhoudao Island, China | 21°30′17.7″ N 108°13′37.1″ E | NW Pacific | MBM286603 | MN133247 | Wang *et al.* (2020) |
| *L. ingens* | Linqiangshidao Island, China | 21°04′46.5″ N 109°06′20.0″ E | NW Pacific | MBM286602 | MN133246 | Wang *et al.* (2020) |
| *L. ingens* | Weizhoudao Island, China | 21°30′17.7″ N 108°13′37.1″ E | NW Pacific | MBM286601 | MN133245 | Wang *et al.* (2020) |
| *L. ingens* | Weizhoudao Island, China | 21°30′17.7″ N 108°13′37.1″ E | NW Pacific | MBM286600 | MN133244 | Wang *et al.* (2020) |
| *L. ingens* | Ko Sichang, Thailand | 13°09′00.0″ N 100°49′12.0″ E | CW Pacific | MBM286599 | MN133243 | Wang *et al.* (2020) |
| *L. medusa* | Chesapeake Bay, Virginia Beach County, Virginia | 36°55′21.4″ N 76°04′21.4″ W | NW Atlantic | – | MK308193 | direct submission |
| *L. medusa* | – | – | – | – | AY040704 | Siddall *et al.* (2001) |
| *Loimia* sp. | Vellar Estuary, Tamil Nadu, India | – | Bengal Gulf, Indic Ocean | – | MG251651 | direct submission |
| *Loimia* sp. | Bardez, Goa, India | 15°34′12.0″ N 73°44′24.0″ E | Arabian Sea, Indian Ocean | – | KX525511 | direct submission |
| *Loimia* sp. | Bardez, Goa, India | 15°34′12.0″ N 73°44′24.0″ E | Arabian Sea, Indian Ocean | – | KX525510 | direct submission |
| *Loimia* sp. | Bardez, Goa, India | 15°34′12.0″ N 73°44′24.0″ E | Arabian Sea, Indian Ocean | – | KX525509 | direct submission |
| *Loimia* sp. | Bardez, Goa, India | 15°34′12.0″ N 73°44′24.0″ E | Arabian Sea, Indian Ocean | – | KX525508 | direct submission |

positions for each sequence pair. A Tamura-Nei model was implemented, as well as the best nucleotide substitution model calculated with IQ-tree for the sequences among those available in MEGA. The rate of variation among sites was modelled with a gamma distribution (shape parameter = 4).

### Morphological analyses

We evaluated the size-related morphological disparity within the specimens of our new species by exploring the position of the small and large morphotypes within the morphospace of all described species of *Loimia*. We successfully coded twelve morphological characters (Supp. file 1: Table S1) traditionally used in the taxonomy of the genus using the literature (mainly original descriptions or type re-descriptions), accounting for the 28 previously known species.

*Loimia annulifilis* (Grube, 1872), *L. bermudensis* Verrill, 1900, *L. contorta* (Ehlers, 1908) and *L. savignyi* McIntosh, 1885 were excluded from the analyses since their descriptions lacked information on some of the relevant characters. All remaining described species were included as one observation in our analyses, except for our new species, whose large and small individuals were included separately to visualize their relative position within the morphospace of *Loimia*. All characters were coded as discrete, with two or more states (Supp. file 1: Table S1). Some of the characters found in descriptions, such as the absence/presence and number of pygidial cirri, the shape of the lappets, as well as the position of the nephridial and genital papillae, were disregarded, as they were not described for a high proportion of the species. For the purposes of this analysis, body size was used to categorized species into large and small, using as length threshold 100 mm the mean of the class range *macrofauna* (2.0–200 mm), as defined for the attribute "qualitative body size" by the WoRMS Editoral Board (Horton *et al.* 2021).

We used the matrix of morphological characters (Supp. file 1: Table S2) to calculate the morphospace of the large (> 100 mm) and the small (< 100 mm) species of *Loimia* using geometrical *n*-dimensional hypervolumes (Blonder *et al.* 2014, 2018; Blonder 2018). The use of hypervolumes to assist species delimitations and taxonomical descriptions has gained momentum in recent years (Koch *et al.* 2016; Mammola *et al.* 2018; Onn *et al.* 2018). Since some of the traits considered here are categorical, we applied a Gower dissimilarity measure to complete the trait matrix and then extracted orthogonal morphological axes through a principal coordinate analysis (Carvalho & Cardoso 2020; Mammola & Cardoso 2020). We delineated hypervolumes with the R package 'hypervolume' (Blonder & Harris 2018). We used the first four principal coordinate axes, which cumulatively explained 74.5% of the variance of our data, and a default bandwidth for each axis. To delineate the hypervolume, we used a Gaussian kernel density estimation (Blonder *et al.* 2014, 2018; Blonder 2018), as it allows us to achieve a probabilistic rather than a binary characterization of the functional space. This probabilistic approach is indeed one of the advantages of using hypervolumes against other functional morphological analyses, such as principal component analysis or convex hull (see Mammola & Cardoso 2020).

Our dataset does not account for the intra-specific variation of all described species of *Loimia*, as each species is limited to one observation coded from the descriptions available in the literature (Supp. file 1: Table S2). The information available in the literature was insufficient to allow an alternative approach, in which the morphological information is coded separately from several individuals per species, due to the variable number of individuals and levels of detail included in each description. Acknowledging that these limitations prevent us from including explicit statistical tests, we provide the main descriptive metrics for the morphospace of *Loimia* and report the relative position of each observation within it with descriptive purposes. Specifically, we calculate the total volume, dispersion, and evenness of the morphospace of all large and small species using the functions kernel.alpha, kernel.dispersion, and kernel.evenness, respectively, available in the R package BAT (Cardoso *et al.* 2015). Furthermore, given that the morphospace of large- and small-sized species largely overlay, we assessed hypervolume overlap with an index of dissimilarity (Mammola 2019). Specifically, we expressed overlap as Beta diversity using the framework proposed by Carvalho & Cardoso (2020) as implemented in the kernel.beta function in BAT (Cardoso *et al.* 2015). Finally, we calculated the Euclidean distance between pairs of observations within the morphospace, as a proxy of the morphological dissimilarity between the two morphotypes of our new species and the remaining species of the genus. All analyses and plots were produced using the statistical software R ver. 1.0.153. All necessary information and scripts are available in Supp. file 1.

## Results

### *Taxonomy*

Phylum Annelida Lamarck, 1809
Family Terebellidae Johnston, 1846
Subfamily Terebellinae Johnston, 1846

Genus ***Loimia*** Malmgren, 1866

#### Type species

*Loimia medusa* (Savigny, 1822) (by original designation).

#### Diagnosis

Based on Carrerette & Nogueira (2015), Nogueira *et al.* (2015) and Wang *et al.* (2020). Eyespots, if present, at basal part of prostomium; lobes on segments 1 and 3 or 1 and 2/3 (in combination of segment 2 and 3), sometimes also on segment 4. Three pairs of branching branchiae, on segments 2–4. Rectangular or trapezoidal mid-ventral shields from segments 2–3 to posterior region where notopodia terminate; last segments of the glandular region usually subdivided by transverse bands. Conical to rectangular notopodia beginning on segment 4, extending for 17 segments, until segment 20; notochaetae all narrowly winged. Neuropodia beginning from segment 5, bearing pectinate uncini, arranged in single rows on segments 5–10 and in double rows on segments 11–20. Genital papillae on segments 6–8. Pygidium smooth to papillate.

***Loimia davidi*** sp. nov.
urn:lsid:zoobank.org:act:D10C6790-B176-4686-B7D3-E7235953AD99
Figs 1–9, Tables 1–4, Supp. file 1

#### Diagnosis

Species of *Loimia* with two pairs of lappets on segments 1 and 3; first pair ventrolateral, with ventral margins in contact midventrally; second pair smaller, lateral. 14–15 ventral shields from segment 2, fused on segments 2 and 3; reddish-brown, with same width in first nine segments, deeply dark brown in following six segments, then progressively narrowing, giving an overall triangular appearance. Ventral shields smooth on segments 2–3 to 10 and with transverse grooves on segments 11 to 16. Uncini pectinate, arranged in a single row on segments 5–10 and in double rows on segments 11–20 (back-to-back), all with a single tooth row over main fang. Thoracic uncini with three and abdominal with four teeth over the main fang (smaller specimens) or all with five teeth over main fang (larger specimen). Thoracic capillary notochaetae alimbate and unilimbate (smaller specimens) or alimbate, unilimbate and bilimbate (larger specimen). Pygidium with either sixteen small, cirriform (smaller specimens) or seven (five dorsolateral, two ventral) long conical (larger specimen) marginal papillae surrounding anus.

#### Etymology

The specific epithet is a homage to David Martin, the first author's second brother, who recently cheated death and recovered from serious psychological illness, but also for his professional and personal achievements and, mainly, for being the person he is.

#### Material examined

**Holotype**

PORTUGAL • 1 ♂ specimen (complete, in three fragments); Açores Archipelago, São Miguel Island, Ilhéu de São Roque – Rostro de Cão; 37°44′37″ N, 25°38′17″ W; 8 m depth; 11 Jul. 2017; D. Martin and

M. Capa leg.; anterior and posterior fragments fixed in 4% formalin/seawater solution, preserved in 70% ethanol; mid-abdominal fragment fixed and preserved in 96% ethanol; CEAB A.P. 935A.

**Paratypes**

PORTUGAL • 1 specimen (complete, in two fragments); same collection data as for holotype; fixed in 4% formalin/seawater solution, preserved in 70% ethanol; CEAB A.P. 935B • 1 specimen (incomplete); same collection data as for holotype; fixed in 4% formalin/seawater solution, preserved in 70% ethanol; MNCN 16.01/19140 • 9 specimens; same collection data as for holotype; fixed and preserved in 96% ethanol; CEAB A.P. 935C • 4 specimens; same collection data as for holotype; fixed in 4% formalin/seawater solution, preserved in 70% ethanol; CEAB A.P. 935D • 4 specimens; same collection data as for holotype; fixed in 4% formalin/seawater solution, preserved in 70% ethanol; MNCN 16.01/19141.

**Comparative material of *L. gigantea* (as *L. ramzega*)**

FRANCE • 2 specs; English Channel, Brittany, Landéda Beach; 48°36′37.7″ N 04°36′24.5″ W; intertidal; 25 Jan. 2012; preserved in 70% ethanol; ARC-*Loimia*-IND2 and -IND5.

## Description

**Holotype**

Complete specimen divided in three fragments, measuring 310 mm long in vivo, with 147 segments; thorax 57 mm long, 12 mm wide when preserved. Body pale brownish in vivo, uniformly beige when preserved (Figs 1A–C, 2A; Supp. file 1: video S1); thorax with ill-defined segmentation dorsally; first three abdominal segments dorsally similar to thoracic ones; remaining abdominal segments with well-marked segmentation and a posterior whitish swelling linking neuropodia dorsally, more visible in posterior-most segments (Figs 1A, 2E). Tentacles long, pale beige in vivo, almost whitish when preserved, with a deep ciliated groove. Tentacular membrane well-defined, increasing in length dorsally, laterally hidden by first pair of lateral lappets (Fig. 2B–C). Eyespots absent. Upper lip conical, with rounded tip, wider than longer; pale brownish, well projecting forward in vivo (Fig. 1C; Supp. file 1: video S1), pale beige, not projecting over first pair of lateral lappets when preserved (Fig. 2B, D). Lower lip not covered by membrane joining first pair of lappets in vivo (Fig. 1C; Supp. file 1: video S1); small, square, covered by membrane joining first pair of lappets when preserved (Fig. 2D). Lateral lappets large, pale brownish to whitish in vivo (Fig. 1A–C; Supp. file 1: video S1), pale beige when preserved (Fig. 2A–D), two pairs, on segment 1 (ventrolateral) and segment 3 (lateral, oblique, with wavy edges, smaller), elephant ear-shaped; first pair laterally reaching notopodia level, ventrally joined by a poorly-developed membrane; second pair separated from base of first pair, laterally hiding segment 2, covering base of first and second branchiae, ending ventrally between first and second ventral shields (Fig. 2B–D). Branchiae on segments 2–4, arborescent, very long, first pair ca ⅙ longer and third pair ⅛ shorter than body width in vivo, with thick stalks and numerous dendritic branches in eight levels, dark red, showing rhythmic contractions in vivo (Fig. 1A–C; Supp. file 1: video S1); whitish when preserved (Fig. 2A–D). Nephridial papillae not seen. Ventral shields on segment 2–9 reddish brown, smooth, with same width; on segments 10–16 deeply dark brown, with transverse grooves, progressively narrowing posteriorly, giving an overall triangular appearance (Fig. 1C; Supp. file 1: video S1). Ventral shields fused on segments 2–3, smooth on segments 2–10 and with transverse grooves on segments 11–16, two on 11–12, 3 on 13, 4 on 14–16) (Fig. 2A). Notopodia from segments 4–20 (17 segments) as swollen, conspicuous lobes, all except first one pale beige to whitish in vivo (Fig. 1A–C; Supp. file 1: video S1), first eleven surrounded by whitish glandular patches (Fig. 1A–B), pale beige when preserved (Fig. 2A). Capillary notochaetae numerous, as long as chaetal lobes, smooth, of three types: alimbate, and uni- and bilimbate (Fig. 3A–C), in J-shaped arrangement. Thoracic neuropodia from segment 5 well developed, pale brownish to whitish in vivo (Fig. 1A–B; Supp. file 1: video S1), uniformly pale beige when preserved (Fig. 2A–C), with numerous uncini arranged in single rows in segments 5–10 and in double rows (back-to-back) in segments 11–20 (Fig. 3D–E), uncini rows ranging from 4 to 6 mm

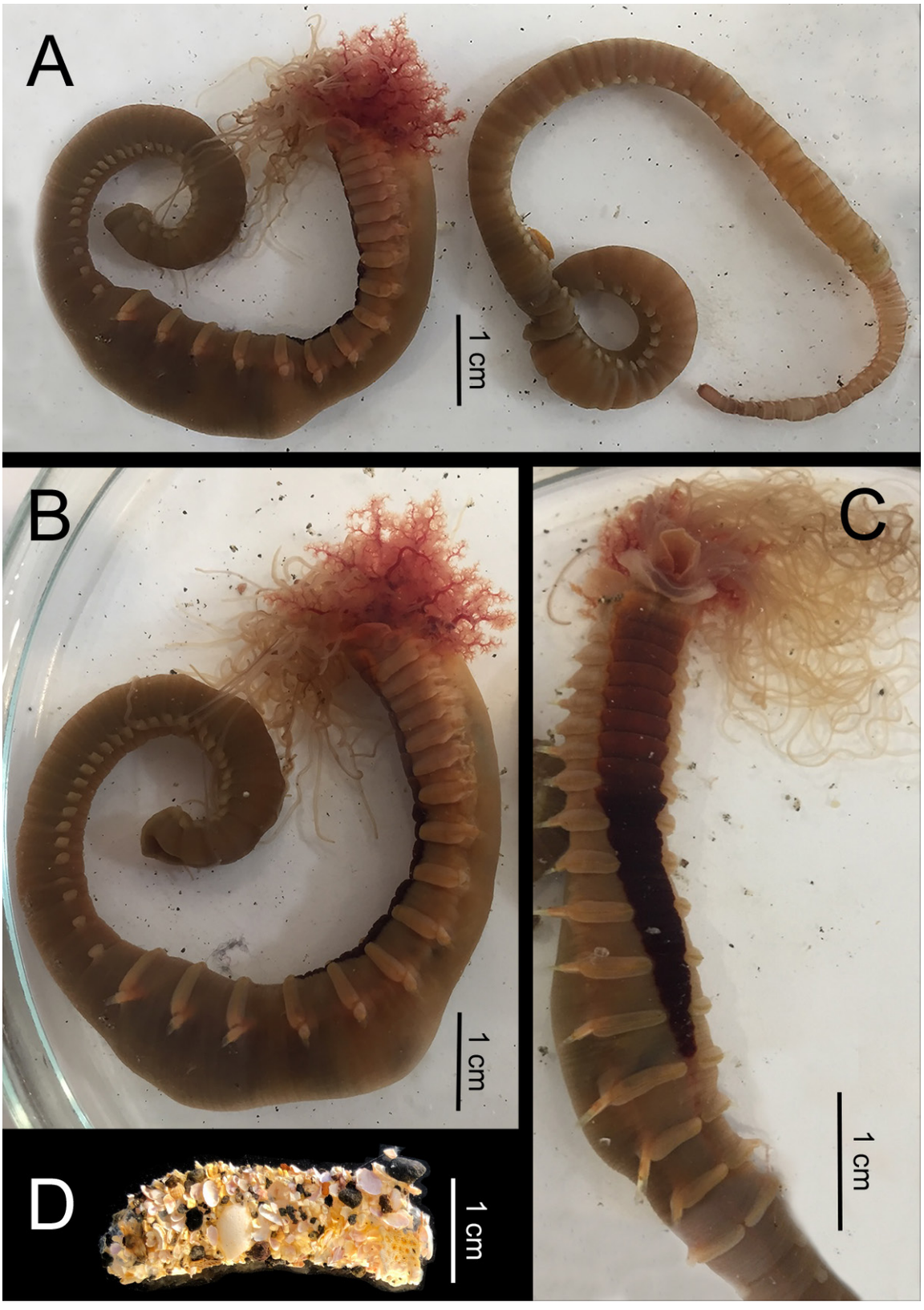



**Fig. 1.** *Loimia davidi* sp. nov., holotype (CEAB A.P. 935A), living. **A**. Entire body in two fragments. **B**. Thorax and anterior abdomen, lateral view. **C**. Thorax, ventral view. **D**. Fragment of tube.

long. Abdominal neuropodia narrow (first abdominal ca 3.6 times as narrow as last thoracic), as long as wide, projecting posteriorly, pale brownish to whitish in vivo (Fig. 1A–B; Supp. file 1: video S1), uniformly pale beige when preserved (Fig. 2A), with uncini in single rows until body end (Fig. 3H). Thoracic uncini measuring ca 120 µm long and 60 µm wide, pectinate, with a crest of five teeth in a single row over main fang, with a curved back three times as long as prow, and reduced heel and dorsal button, with anterior filament long, projected downwards (Figs 3E–F, 4A). Abdominal uncini pectinate, measuring ca 105 µm long and 55 µm wide, with a crest of five teeth in a single row over main fang (Fig. 3I), connected to basis of parapodia by long, hyaline ligaments (Fig. 3H), similar in shape to thoracic ones, with a less curved back, 2.5 times as long as prow, heel inconspicuous, and strongly reduced dorsal button (Fig. 3I). Regenerating posterior end, abruptly differing from previous segments, with shorter and narrower segments, dark reddish with pale beige posterior swellings linking bases of neuropodia (Fig. 2E–F). Pygidium with terminal anus, surrounded by eighteen small, almost cirriform terminal papillae, dorso-laterally broadly grouped in pairs (12), ventrolaterally individual (6) (Fig. 2F). Tube at least four times as long as body length, formed by aggregated sand grains, shell fragments and

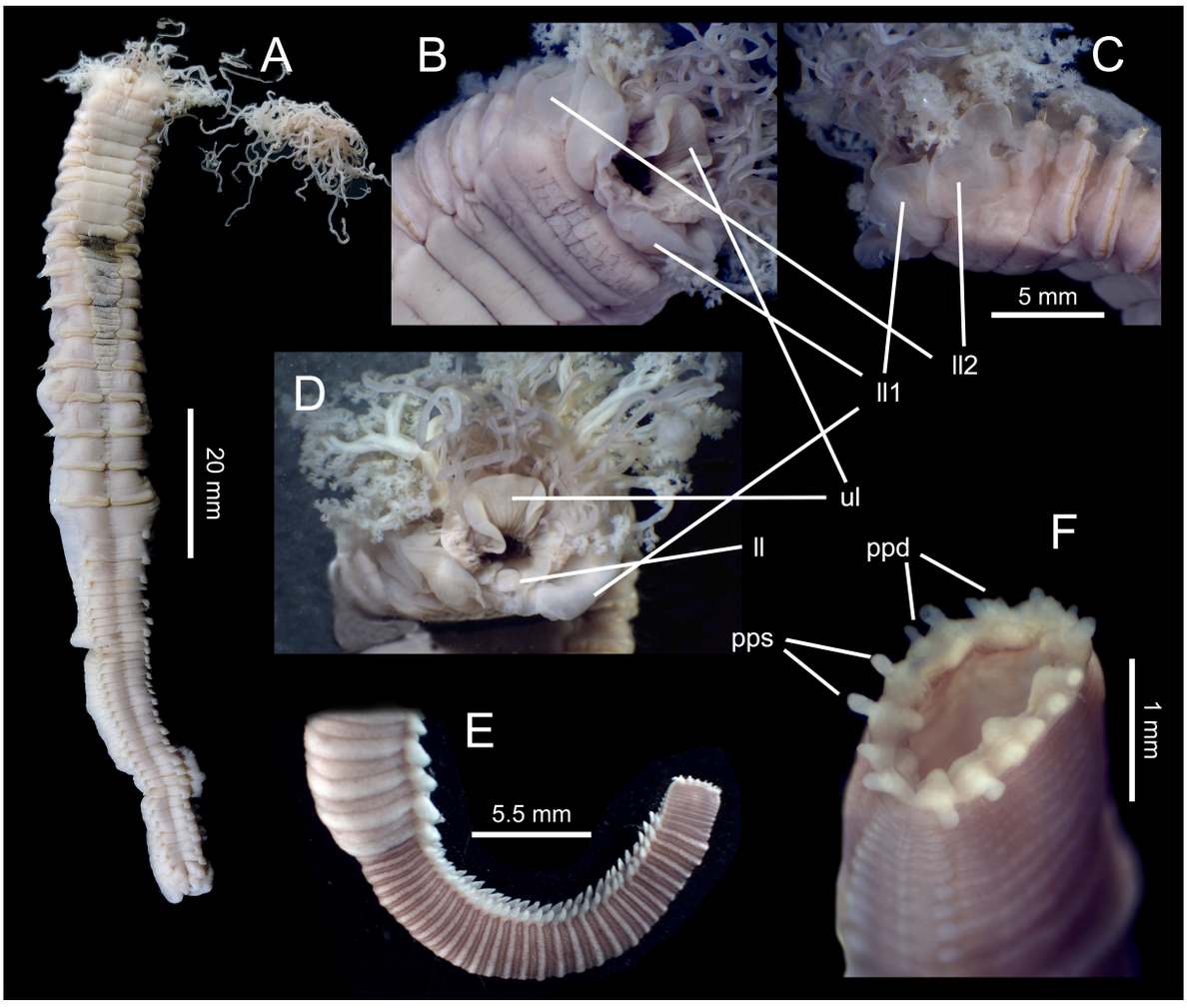



**Fig. 2.** *Loimia davidi* sp. nov., holotype (CEAB A.P. 935A), preserved. **A**. Anterior region, ventral view. **B**. Detail of anterior end, ventral view. **C**. Detail of anterior end, lateral view. **D**. Detail of anterior end, frontal view. **E**. Entire view of the regenerating posterior end. **F**. Detail of the pygidium showing the anal papillae. Abbreviations: ul = upper lip; ll = lower lip; ll1 = first pair of lateral lappets; ll2 = second pair of lateral lappets; ppd = double pygidial papillae; pps = simple pygidial papillae.

other calcareous debris covering a thick, smooth, inner mucus layer (Fig. 1D), partly hidden under big boulders. Coelom filled with oocytes measuring ca 60 µm in diameter.

**Paratypes**

Based on paratype CEAB A.P. 936B (with variation in the other small paratypes between brackets). Body divided in two fragments, 41 mm long with 77 segments in total (other paratypes were all anterior fragments, including thorax and several abdominal segments). Thorax 19 mm (8–20 mm) long and 3.6 mm (2–5 mm) wide; with ill-defined segmentation dorsally; first six abdominal segments dorsally similar to thoracic ones, but segmentation better defined; remaining abdominal segments well marked, long, pale reddish, with a posterior whitish swelling dorsally linking neuropodia (Fig. 5A). Tentacles few in number, with U-shaped cross-section. Tentacular membrane well defined, poorly developed on ventral side; laterally hidden by first pair of lateral lappets (Fig. 5D); eyespots present in some specimens, progressively decreasing in diameter when more dorsal (Fig. 5F). Upper lip well projecting forward, wider than long; thicker at base, almost completely hidden ventrally by first pair of lateral lappets

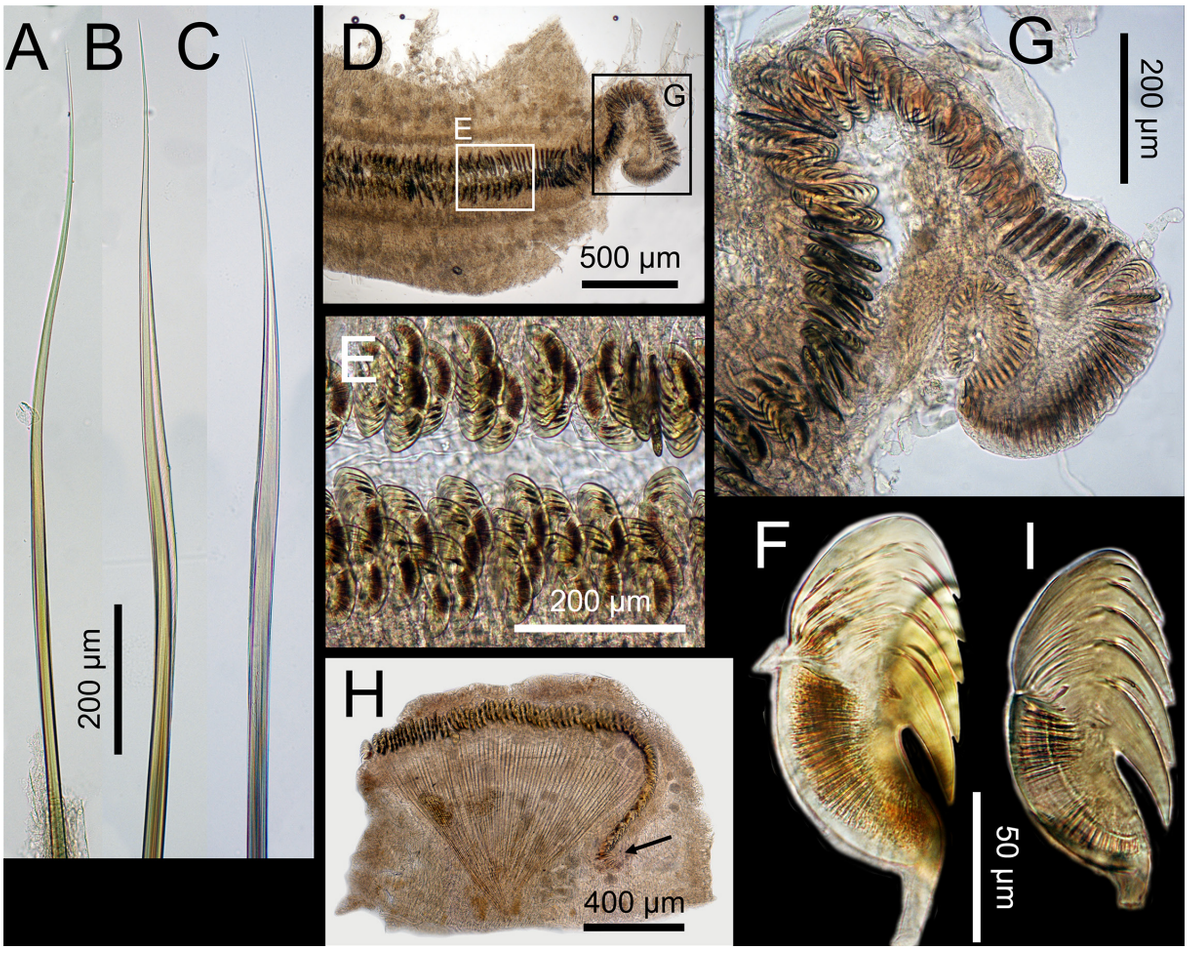



**Fig. 3.** *Loimia davidi* sp. nov., holotype (CEAB A.P. 935A), preserved. **A–C**. Chaetae from chaetiger 11. **A**. Alimbate capillary chaeta. **B**. Unilimbate capillary chaeta. **C**. Bilimbate capillary chaeta. — **D–G**. Chaetiger 12. **D**. Ventro-lateral section of thoracic parapodium. **E**. Uncini of the same, arranged in two rows, back to back. **F**. Single thoracic uncinus of the same. **G**. Detail of the uncinal growing region of the same. — **H–I**. Segment 25. **H**. Abdominal parapodium (arrow pointing to uncinal growing zone). **I**. Single abdominal uncinus of the same.

(Fig. 5B, D–E). Lower lip ¼ times as long as upper lip, swollen, with conical tip, hidden ventrally by membrane connecting first pair of lateral lappets (Fig. 5E). Lateral lappets large, discontinuous, two pairs, on segments 1 and 3 (Fig. 5A–E); first pair quadrangular, laterally reaching notopodia level, with a well-developed joining membrane; second pair separated from base of first pair, ⅔ times as large as first, laterally hiding segment 2, covering base of first branchiae, ending ventrally between first and second ventral shields. Three pairs of branched branchiae (Fig. 5C) whitish (preserved material), starting from segment 2; first pair ca ⅓ as long as body width, third pair ca 0.8 times as long as body width; branchiae with thick stalks, with many dendritic branches arranged in four levels. Nephridial papillae not seen. First twelve notopodia surrounded by whitish glandular patches (Fig. 5A); fourteen ventral shields, starting from segment 2, fused on segments 2–3, wider than long on segments 2–11; on segments 2–10 smooth, all about the same size; on segments 11–13 (11–12 in some specimens) with one transverse groove, then two transverse grooves on segment 14 and more than two on segment 15 (non-distinguishable in smallest specimen); abdomen smooth ventrally until pygidium (Fig. 5A). Notopodia from segment 4, extending through segment 20 as swollen, conspicuous lobes (Fig. 5A). Notochaetae of two types within same fascicle, alimbate and narrowly unilimbate capillaries, similar in length (Fig. 6A–B), in J-shaped arrangement. Thoracic neuropodia starting from segment 5, first seven ⅔ times as large as posterior ones, with uncini arranged in single rows in segments 5–10, and in double rows (back-to-back position)

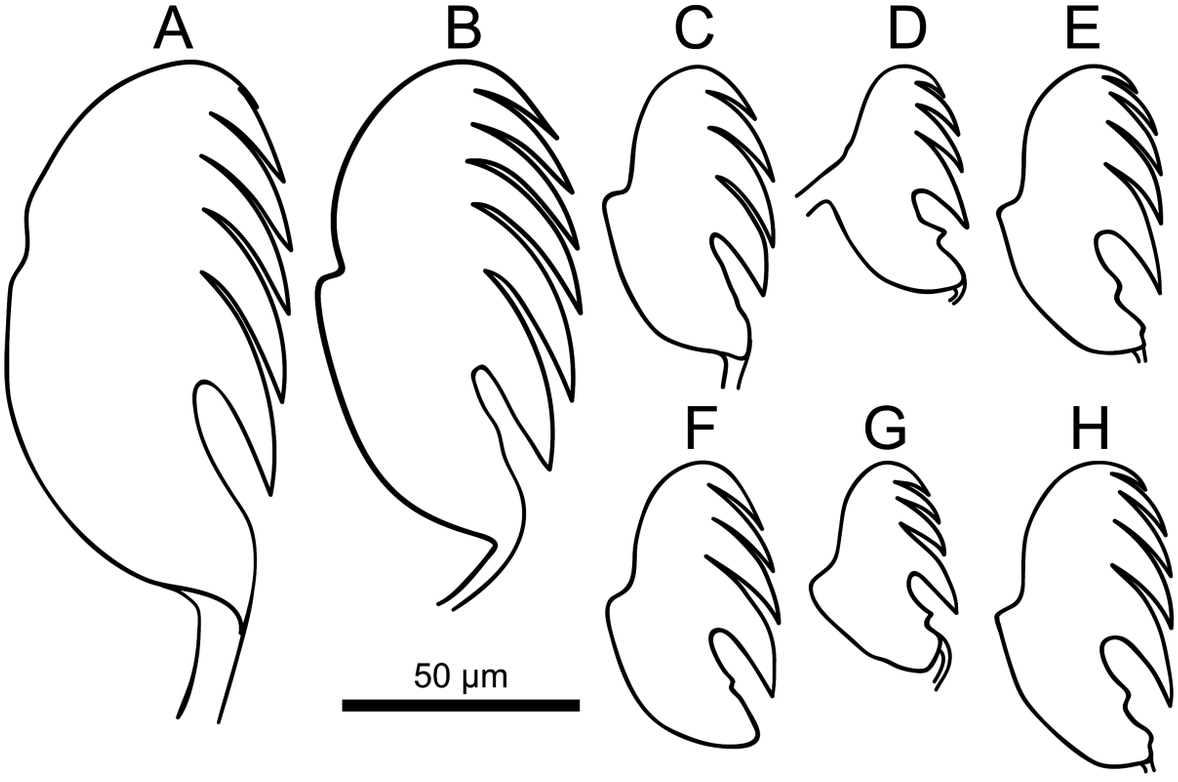



**Fig. 4.** Schematic drawings of the thoracic uncini. **A**. *Loimia davidi* sp. nov., holotype (CEAB A.P. 935A). **B**. *L. ramzega* Lavesque, Bonifácio, Londoño-Mesa, Le Garrec & Grall, 2017, redrawn after Lavesque *et al*. (2017). **C**. *L. davidi* sp. nov., paratype (CEAB A.P. 935B). **D**. *L. salazari* Londoño-Mesa & Carrera-Parra, 2005, redrawn after Londoño-Mesa & Carrera-Parra (2005). **E**. *L. minuta* Treadwell, 1929 from Florida (USA), redrawn after Londoño-Mesa (2009). **F**. *L. minuta* from the Mexican Caribbean, redrawn after Londoño-Mesa & Carrera-Parra (2005). **G**. *L. medusa* (Savigny, 1822) from the Persian Gulf, redrawn after Hutchings & Glasby (1995). **H**. *L. medusa* from the Mexican Caribbean, redrawn after Londoño-Mesa & Carrera-Parra (2005).

in segments 11–20 (Fig. 6C). Abdominal neuropodia narrow (first abdominal ca 4.1 times as broad as last thoracic), half as long as wide, projecting posteriorly, with uncini in single rows until pygidium. Thoracic uncini measuring ca 60 µm long and 35 µm wide, pectinate, with a crest of three teeth in a single row over main fang, with a curved back twice as long as prow, well-marked heel and reduced dorsal button, with anterior filament long, projected downwards (Figs 4C, 6D). Abdominal uncini ca 46 µm long and 30 µm wide, similar in shape to thoracic ones, with a crest of four teeth in a single row over main fang (Fig. 6E). Pygidium with terminal, rounded anus, surrounded by seven long, conical terminal papillae with a well-defined base, forming two clearly separated groups of five dorsolateral and two ventral papillae (Fig. 5G–H). Tube not seen.

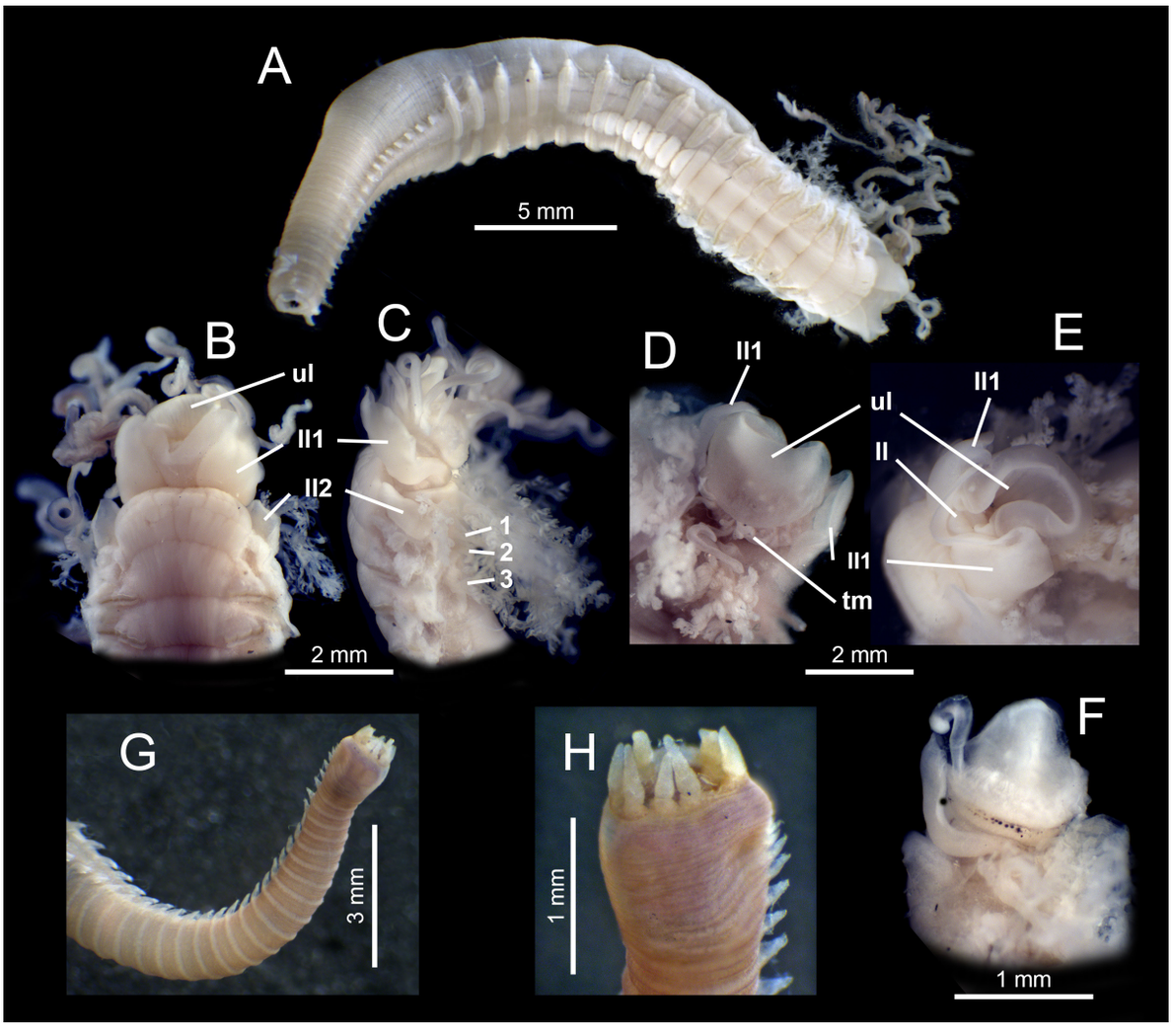



**Fig. 5.** *Loimia davidi* sp. nov. **A–C, G–H**. Paratype CEAB A.P. 935B. **D–F**. Paratype MNCN 16.01/19140. **A**. Anterior fragment in ventral view. **B**. Anterior end in ventral view. **C**. Anterior end in lateral view. **D**. Anterior end in dorsal view. **E**. Anterior end in frontal view. **F**. Anterior end in lateral view, showing ocular spots. **G**. Posterior end in dorsal view. **H**. Detail of the pygidial papillae. Abbreviations: ll = lower lip; ll1 = first pair of lateral lappets; ll2 = second pair of lateral lappets; tm = tentacular membrane; ul = upper lip; 1–3 = branchiae.

**Remarks**

**Larger vs smaller specimens of *L. davidi* sp. nov.**

The specimens of *L. davidi* sp. nov. show obvious morphological differences, which in other circumstances could have been considered as representing different species (Table 2). This is the reason why we present the comparisons of both morphotypes with other species of the genus separated in the next two sections. However, most of these differences appear to be size-related to some extent, since the largest specimen always shows larger or more numerous structures, such as branchiae, capillary chaetae, and uncini. The only differences apparently non size-related are the presence of eyes and the length of terminal pygidial papillae. However, eyes are subdermal and may become hidden by the thicker tegument of the larger specimen. As for the pygidial papillae, they clearly have distinct shapes, but also are more numerous in the largest specimen and proportionally longer in the smaller ones. Nevertheless, the giant specimen was regenerating its posterior end, having the last ca 29 segments thinner and shorter than the previous ones (Figs 1A, 2E). Although we suggest that the shape and smaller size of its terminal pygidial papillae (Fig. 2F) may be related to the regenerating process, this cannot be confirmed because there is only one large specimen avilable.

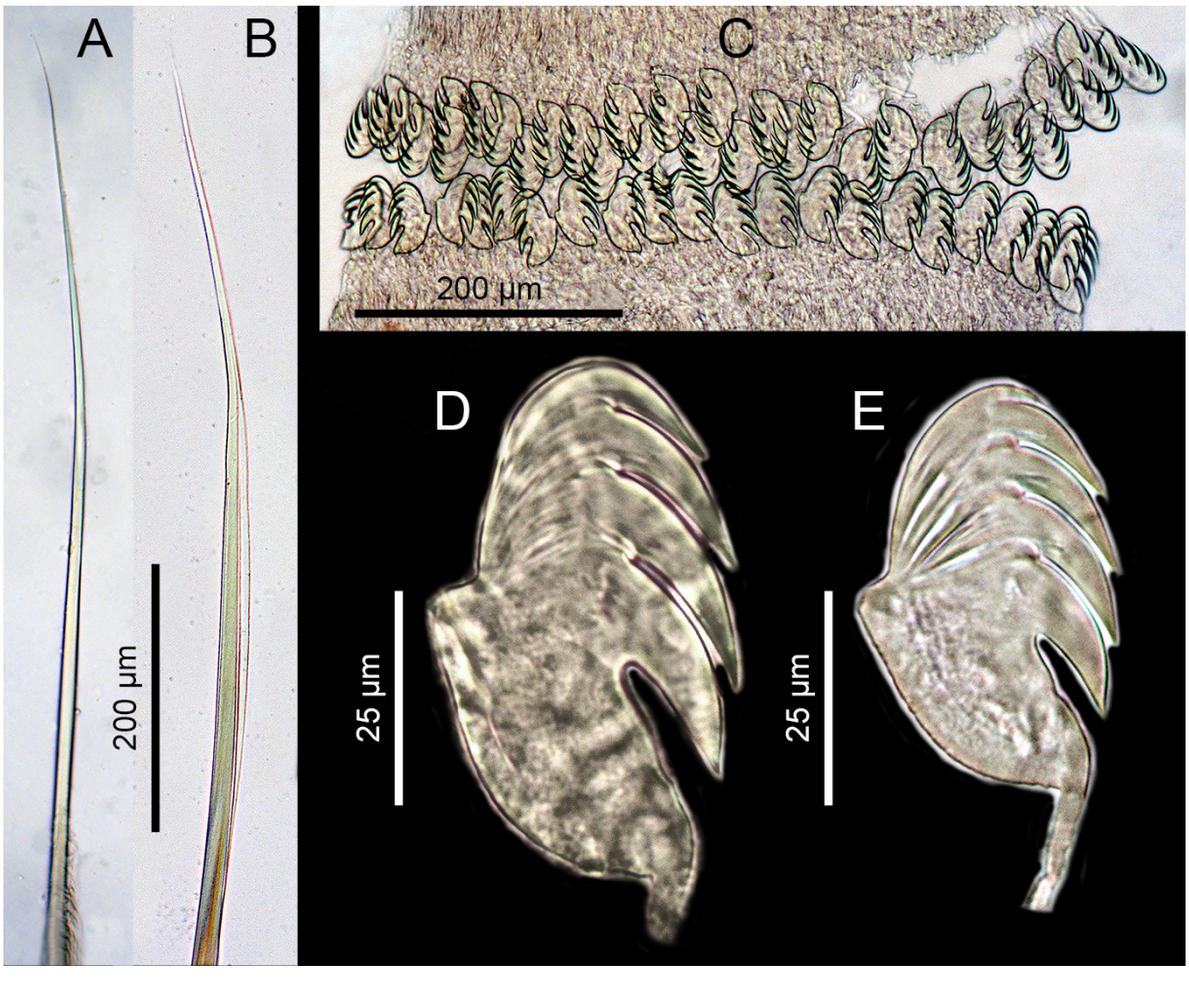



**Fig. 6.** *Loimia davidi* sp. nov., paratype MNCN 16.01/19140. **A**. Alimbate capillary chaeta. **B**. Unilimbate capillary chaeta. **C**. Position of the thoracic uncini from segment 10. **D**. Single thoracic uncinus from segment 10 (thorax). **E**. Single abdominal uncinus from segment 22 (abdomen).

**Table 2.** Summary of the morphological characters diferring between larger and smaller specimens of *Loimia davidi* sp. nov.

| Characters | Larger | Smaller |
|---|---|---|
| Thorax length | 57 mm | 19 mm |
| Thorax width | 12 mm | 3.6 mm |
| Tentacles | very abundant | scarce |
| Eyespots | absent | present in some specimens, numerous, diameter progressively decreasing dorsalwards |
| Upper lip | tongue-shaped, wider than longer, not projecting over first pair of lateral lappets | spoon-like, well projecting forward, wider than longer; thicker at base, almost completely hidden ventrally by first pair of lateral lappets |
| Lower lip | square | swollen, with conical tip |
| Lateral lappets | elephant ear-shaped, similar in size, first pair with a poorly-developed joining membrane | quadrangular, with different size, first pair with a well-developed joining membrane |
| Branchiae | dendritic branches arranged in 8 levels | dendritic branches arranged in 4 levels |
| Presence of ventral shields | from segment 2, on 15 segments | from segment 2, on 14 segments |
| Anterior ventral shields | 9, similar width, wider than longer | 10, similar width, wider than longer, but 5–7 clearly narrower |
| Posterior ventral shields | 6, darker, progressively narrowing, giving an overall triangular appearance | 4, whitish, progressively narrowing, giving an overall triangular appearance |
| Fused ventral shields | segments 2–3 | segments 2–3 |
| Transversally non-grooved ventral shields | segments 2–10 | segments 2–10 |
| Ventral shields with 2 transversal grooves | segments 11–12 | segments 11–13 |
| Ventral shields with 3 transversal grooves | segment 13 | segment 14 |
| Ventral shields with > 3 transversal grooves | segments 14–16 | segment 15 |
| Notopodial whitish glandular patches | on first 11 segments | on first 12 segments |
| Types of capillary notochaetae | 3, alimbate, and uni- and bilimbate | 2, alimbate and unilimbate |
| Neuropodia | from segment 5, well-developed | from segment 5, 7 anterior pairs smaller |
| Size of thoracic uncini | 120 µm long, 60 µm wide | 60 µm long, 35 µm wide |
| Crest of thoracic uncini | 5 teeth over main fang, upper one difficult to see | 3 teeth over main fang |
| Heel of thoracic uncini | round, reduced | well-defined, triangular |
| Dorsal button of thoracic uncini | present, very reduced | well-marked |
| Abdomen | single specimen regenerating posterior end | all specimens except one incomplete posteriorly |
| Anterior abdominal segments | 3, similar to thoracic segments | 6, similar to thoracic segment, with better defined segmentation |
| Size of abdominal uncini | 105 µm long, 55 µm wide | 46 µm long, 30 µm wide |
| Crest of abdominal uncini | 5 teeth over main fang, upper one much smaller | 4 teeth over main fang |
| Back of abdominal uncini | slightly curved, 2.5 times as long as prow | curved, 3 times longer as long as prow |
| Heel of abdominal uncini | inconspicuous | well-defined, triangular |
| Dorsal button of abdominal uncini | strongly reduced | well-marked |
| Anus | terminal, surrounded by 18 terminal papillae | terminal, round, surrounded by 7 terminal papillae |
| Anal terminal papillae | small, cirriform; 12 dorso-laterally, broadly grouped in pairs; 6 ventro-laterally, individual | long, conical, forming 2 clearly separated groups of 5 dorsolateral and 2 ventral papillae |

Once dissected, the parapodia of the largest specimen show lateral zones with growing uncini both in the thorax (Fig. 3D–E) and in the abdomen (Fig. 3H). In thoracic parapodia, the uncini are arranged in single rows in the growing zones, even in those parapodia with double rows of normal uncini (Fig. 3E). Similar growing zones are not seen in the small specimens, likely because they are too small to be distinguished. The living largest specimen rhythmically contracted its branchial tips (Supp. file 1: video S1), likely increasing water renewal. Branchial contractions cannot be confirmed for our small specimens (none of them were observed in vivo), and neither have any been previously reported for other giant specimens of *Loimia* (Montagu 1819; Lavesque *et al.* 2017). Conversely, Wilson (1928) reported contractile branchiae and clearly visible red blood pulsations through the blood vessels in the early benthic stages of *Loimia* from the English Channel.

It would be interesting to examine more material – especially large animals – to further assess the variation/homogeneity of all these particular morphological characters, which in most cases have been considered as key for species diagnosis.

**Larger specimen of *L. davidi* sp. nov. vs other species of *Loimia* Malmgren, 1866**

The larger specimen of *L. davidi* sp. nov. is distinguished from other congeners by a unique combination of features: (1) two pairs of lappets on segments 1 and 3, first pair almost reaching each other midventrally and second pair laterally, not joining midventrally; (2) long arborescent branchiae with up to eight levels of branches; (3) three kinds of notochaetae in thoracic segments including alimbate, unilimbate and bilimbate capillaries; and (4) thoracic and abdominal uncini with five teeth in a single longitudinal row over main fang (Table 3; Supp. file 1: Table S3). The holotype resembles the described specimens of *L. gigantea* from Brittany (France) both in size and overall morphology, but also in bearing two additional types of capillary notochaetae together with the typical smooth ones, instead of none or one in all remaining species of *Loimia* (Table 3; Supp. file 1: Table S3). However, the presence of three types of capillary chaetae is only known in these very large specimens of *Loimia*, whereas the smaller specimens of *L. davidi* sp. nov. show only two types, thus casting serious doubts on the taxonomic value of this character.

The larger specimen of *L. davidi* sp. nov. differs from *L. gigantea* in having the first pair of lateral lappets more developed (second pair more developed in *L. gigantea*), lappets uniformly pale brownish to whitish in vivo (first pair with a red margin and second pair entirely red in *L. gigantea*). Lateral lappets may show some variability among Terebellidae, although they have traditionally been used to distinguish species (e.g., Jirkov 2020). Thus, we consider the observed differences as relevant enough to be mentioned here. These two species also differ in the absence of abdominal dark spots (present in *L. gigantea*), branchiae arranged in eight levels (five in *L. gigantea*), fifteen ventral shields (sixteen in *L. gigantea*), and uncini ca 120 µm long with slightly marked, round heel and upper-most tooth very small, often difficult to distinguish (100 µm, well-marked, angular heel and well-defined upper tooth in *L. gigantea*) (Fig. 4A–B). Moreover, although being of doubtful value due to its regenerating posterior end, the larger specimen of *L. davidi* sp. nov. has 18 terminal pygidial papillae (14 in *L. gigantea*). In addition, this specimen was found subtidally, partly hidden under big boulders, and its tube is composed of sand grains and shell remains, while *L. gigantea* occurred intertidally and, in addition to sand and shell fragments, their tubes characteristically show macroalgal filaments attached to the emerging portion (absent in the tube of the larger specimen of *L. davidi* sp. nov.). Considering that we only found one large specimen of *L. davidi* sp. nov., we cannot confirm whether the observed differences in tube structure can be considered species-specific.

We have found two additional morphological differences between the larger specimen of *L. davidi* sp. nov. and *L. gigantea* after the re-examination of the paratypes of the latter, not mentioned in its original description (Lavesque *et al.* 2017). First, the segmentation in *L. gigantea* is clearly defined dorsally all along the body, with all segments transversally divided by several grooves and at least the

**Table 3.** Comparison of lateral lappets and number of teeth (including the main fang and the upper teeth) in thoracic and abdominal uncini of the species of *Loimia* Malmgren, 1866 considered as valid in the present study. Abbreviation: r = reduced.

| Species | Lateral lappets | Thoracic uncini | Abdominal uncini | Location | Original description |
|---|---|---|---|---|---|
| *L. annulifilis* | | | | | Grube (1872) |
| *L. arborea* | 1 and 2/3 | 5(6) | 6(7) | Japan | Moore (1903) |
| *L. armata* | | | | | Carrerette & Nogueira (2015) |
| *L. bandera* | | | | | Hutchings (1990) |
| *L. batilla* | 1 and 2/3 | 6 | 7 | Australia | Hutchings & Glasby (1988) |
| *L. bermudensis* | 1 and 3 | 5–6(6r) | 5–6(6r) | Bermuda | Verrill (1900) |
| *L. borealis* | | | | | Wang *et al.* (2020) |
| *L. brasiliensis* | | | | | Carrerette & Nogueira (2015) |
| *L. contorta* | | | | | Ehlers (1908) |
| *L. crassifilis* | | | | | Grube (1878) |
| *L. davidi* sp. nov. (larger) | 1 and 3 | 6(6r) | 6(6r) | Açores Archipelago | This paper |
| *L. davidi* sp. nov. (smaller) | 1 and 3 | 4 | 5 | Açores Archipelago | This paper |
| *L. decora* | 1 and 2/3 | 5 | 5 | Sri Lanka | Pillai (1961) |
| *L. gigantea* | 1 and 3 | 6(5) | 6(5) | Atlantic (France) | Montagu (1819), redescribed by Lavesque *et al*. (2017) |
| *L. grubei* | 1 and 2/3 | 5 | 5–6 | Philippines | Holthe (1986) |
| *L. ingens* | | | | | Grube (1878) |
| *L. juani* | | | | | Nogueira, Hutchings & Carrerette (2015) |
| *L. keablei* | | | | | Nogueira *et al*. (2015) |
| *L. macrobranchia* | | | | | Wang *et al.* (2020) |
| *L. medusa* | 1 and 3 | 4–5 | 4–5 | Persian Gulf / Red Sea | Savigny (1822) |
| *L. medusa angustescutata* | | | | | Willey (1905) |
| *L. megaoculata* | | | | | Carrerette & Nogueira (2015) |
| *L. minuta* | 1 and 3 | 5 | 6 | Caribbean (Mexico) | Treadwell (1929) |
| *L. nigrifilis* | | | | | Caullery (1944) |
| *L. ochracea* | | | | | Grube (1877) |
| *L. pseudotriloba* | | | | | Nogueira *et al.* (2015) |
| *L. salazari* | 1 and 3 | 4 | 4 | Caribbean (Venezuela) | Londoño-Mesa & Carrera-Parra (2005) |
| *L. savignyi* | | | | | McIntosh (1885) |
| *L. savignyi trussanica* | | | | | Annenkova (1925) |
| *L. triloba* | 1 (3 and 4) | 5(6) | 5(6) | Australia | Hutchings & Glasby (1988) |
| *L. tuberculata* | | | | | Nogueira *et al.* (2015) |
| *L. turgida* | | | | | Andrews (1891) |
| *L. variegata* | | | | | Grube (1869) |
| *L. verrucosa* | 1 and 3 | 7 | 7 | Indonesia | Caullery (1944) |
| *L. viridis* | 1 and 3 | 7–8 | 7–8 | Massachusetts (USA) | Moore (1903) |

median one entirely splitting each segment. This is particularly evident in the abdominal segments, where the main transversal groove divides each segment into two equal parts. Also, there are no traces of a swelling dorsally linking the abdominal parapodia. In contrast, the body segmentation in the larger specimen of *L. davidi* sp. nov. is characteristically ill-defined dorsally in the thoracic and first three abdominal segments, and well-marked with a posterior whitish swelling dorsally linking the neuropodia

in all remaining abdominal segments (including those in the regenerating region). Second, in *L. gigantea*, the uncini are arranged in typical back-to-back double rows (Fig. 7A) and irregularly distributed in the abdominal parapodia (Fig. 7B–C), whereas in the larger specimen of *L. davidi* sp. nov. the abdominal uncini are arranged in a single row (Fig. 3H). The lateral zones with growing uncini observed in the larger specimen of *L. davidi* sp. nov. (Fig. 3D–E, H) are also present in *L. gigantea* (Fig. 7A–B) and typically also occur in the species of *Axionice* (Jirkov & Leontovich 2017).

**Smaller specimens of *L. davidi* sp. nov. vs other species of *Loimia* Malmgren, 1866**

The smaller specimens of *L. davidi* sp. nov. are distinguished from other congeners by a unique combination of features: (1) presence of eyespots in the tentacular membrane; (2) two pairs of similar-

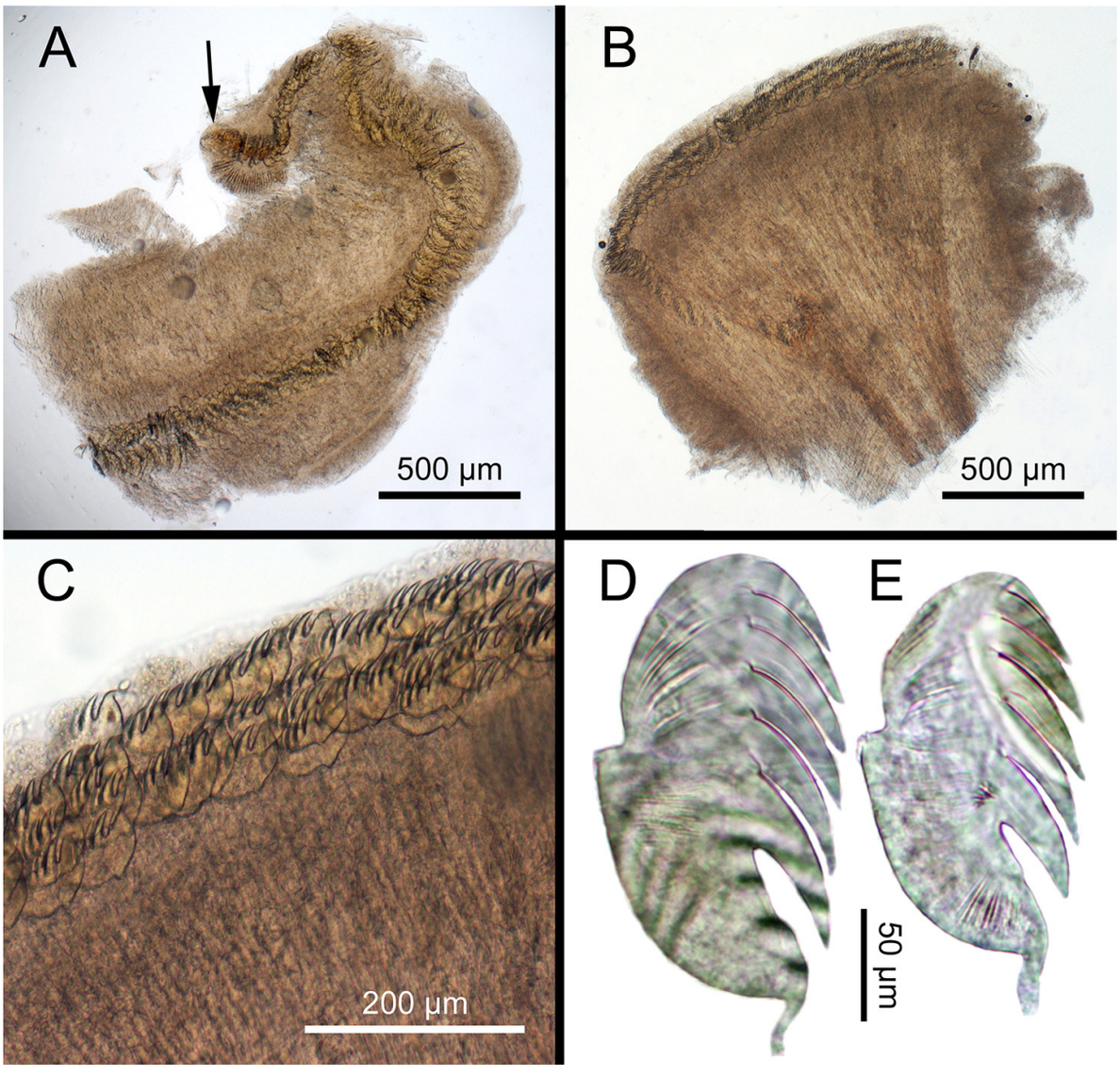



**Fig. 7.** *Loimia gigantea* (Montagu, 1819), ARC-Loimia-IND2. **A**. Dorsolateral section of thoracic neuropodium 12, showing the uncinal growing zone (black arrow). **B**. View of entire abdominal neuropodium 4. **C**. Detail of the uncinal arrangement of abdominal neuropodium 4. **D**. Uncinus from thoracic neuropodium 8. **E**. Uncinus from abdominal neuropodium 4.

sized lappets on segments 1 and 3, first pair ventral and almost reaching each other midventrally and second pair lateral; (3) two kinds of notochaetae in thoracic segments including alimbate and unilimbate capillaries; and (4) thoracic and abdominal uncini with three and four teeth, respectively, in a single longitudinal row over main fang (Table 3; Supp. file 1: Table S3).

These small specimens resemble *L. medusa*, as redescribed by Hutchings & Glasby (1995), in the shape and size of uncini, although the latter has a dorsal button three times longer, relative to uncinus length (Fig. 4C, G). However, *L. davidi* sp. nov. lacks visible pigmented red spots on the tentacles (present in *L. medusa*), possesses alimbate and unilimbate capillary notochaetae (narrow bilimbate in *L. medusa*), has fourteen ventral shields (twelve in *L. medusa*) and bears seven terminal papillae, forming two groups on the pygidium (absent in *L. medusa*). The specimens from the Mexican Caribbean identified and described as *L. medusa* by Londoño-Mesa & Carrera-Parra (2005) were considered as morphologically indistinguishable from the upper Persian Gulf neotype designated by Hutchings & Glasby (1995). However, the number of ventral shields in these Caribbean specimens varied between eleven and sixteen (twelve in Persian *L. medusa*), with those from segments 2, 3 and part of 4 being almost fused and all of them being entire, not divided by transversal grooves in the Caribbean specimens (Londoño-Mesa & Carrera-Parra 2005) and entirely fused from 2 to 4 in the Persian specimens (Hutchings & Glasby 1995). Moreover, the uncini of the Caribbean specimens were slightly longer than those of the Persian *L. medusa* and of *L. davidi* sp. nov. (Fig. 4C, G–H). Considering these differences and the distance between the Caribbean Sea and the Persian Gulf, we suggest that the Caribbean specimens probably represent a different species that merits further analysis.

The smaller specimens of *L. davidi* sp. nov. resemble *Loimia salazari* Londoño-Mesa & Carrera-Parra, 2005 and *Loimia minuta* Treadwell, 1929 in having two types of capillary notochaetae which, in addition to the arrangement of the lateral lappets and number of uncinal teeth, clearly distinguishes these species from other congeners (Table 3). However, *L. davidi* sp. nov. has equally long unilimbate and alimbate capillary notochaetae (longer narrowly bilimbate and shorter alimbate in *L. salazari*), fourteen ventral shields (eighteen in *L. salazari*) transversally grooved from the ninth shield (thirteenth in *L. salazari*), and seven terminal pygidial papillae in two groups (fourteen small papillae in *L. salazari*). *Loimia salazari* was described as the only *Loimia* bearing uncini with posterior processes in the anterior thoracic neuropodia, a feature that is instead typical of genera such as *Pista* Malmgren, 1866, *Lanicides* Hessle, 1917, *Eupistella* Chamberlin, 1919, or *Opisthopista* Caullery, 1944. Also, the shape of the uncini was originally described as pectinate (Londoño-Mesa & Carrera-Parra 2005) and later as avicular (Lavesque *et al*. 2017). Accordingly, the generic assignment of *L. salazari* is here considered doubtful. *Loimia minuta* has ten ventral shields, transversally grooved from the seventh one, and a pygidium with six long digitate terminal papillae. Moreover, the species descriptions across geographical areas markedly differed in the presence of different types of notochaetae. The type material (from Florida) had asymmetrically bilimbate capillaries with two different lengths (Londoño-Mesa 2009), whereas the Mexican Caribbean specimens had long, thick bilimbate and short, thin, pointed alimbate capillaries (Londoño-Mesa & Carrera-Parra 2005). Whether this is connected with the size of the respective specimens is not discussed by Londoño-Mesa & Carrera-Parra (2005) and, thus, neither herein. Finally, the uncini of *L. davidi* sp. nov. are overall similar in shape and size to those *L. minuta*, from both Florida and Mexican Caribbean populations (Fig. 4C–F).

**Distribution**

Sandy patches among boulders and seaweeds, in shallow subtidal waters of São Miguel Island, Açores, Portugal (Atlantic Ocean). It represents the first report of the genus *Loimia* in the Açores Archipelago.

### *Molecular analyses*

The alignment of 31 sequences of *cox1* of *Loimia* and the outgroup is 402 bp long and includes 138 parsimony informative sites (Fig. 8). The three sequences from the Açores nest in a well-supported clade, internally separated by short branches (Fig. 8, Table 4). Indeed, the genetic divergences within this clade are 1.1% (between the small specimens) and 2.1–2.2% (between large and small specimens). In contrast, they diverge by 16.4–36.1% from the other species of *Loimia* included in the analyses (Table 4).

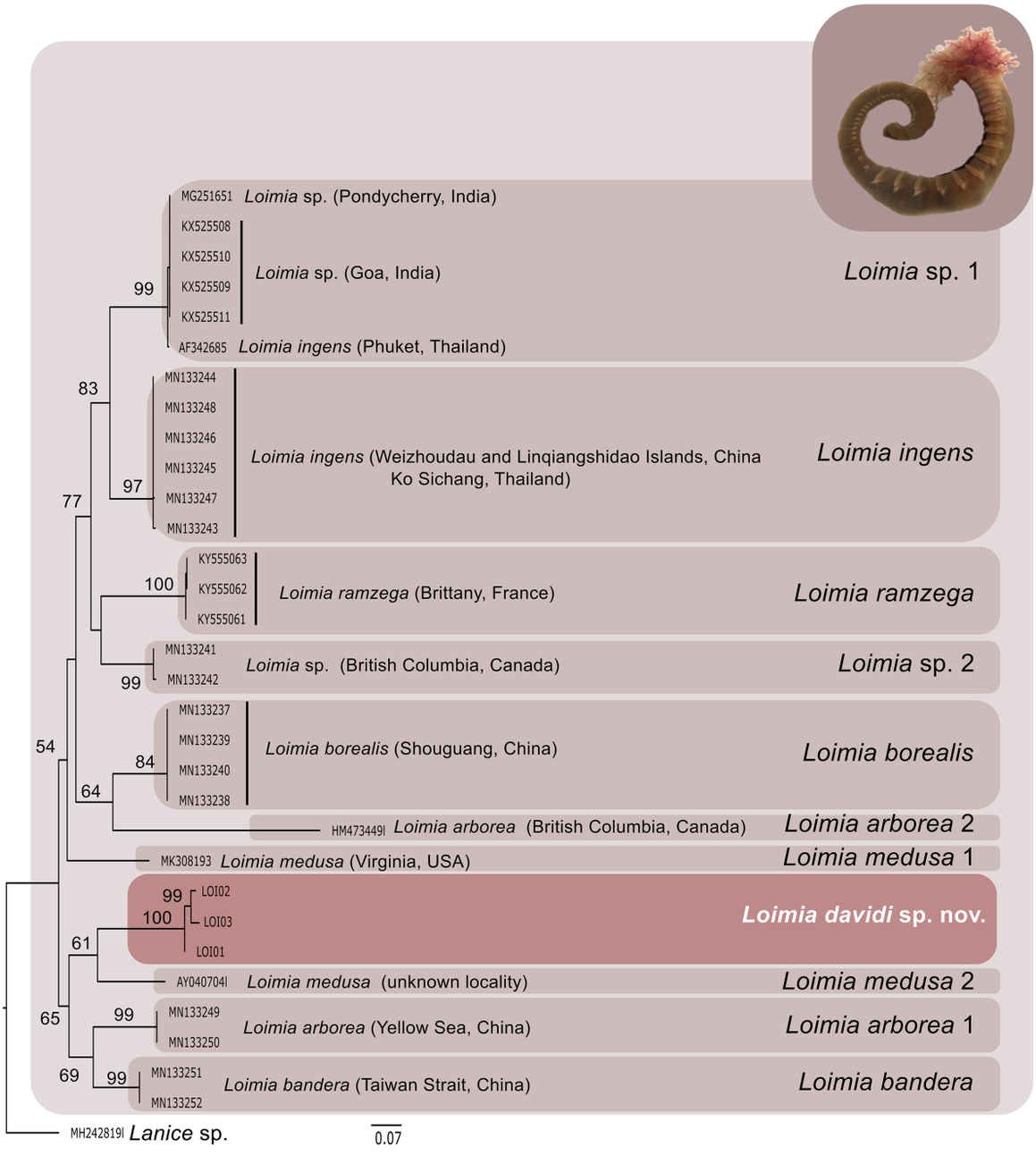



**Fig. 8.** Phylogenetic reconstruction after Maximum Likelihood analyses of the *cox1* fragment. Bootstrap support values (BS) above nodes.

**Table 4.** Estimates of evolutionary divergence over sequence pairs between groups (species), showing the number of base substitutions per site from averaging over all sequence pairs between groups. Analyses were conducted using p-distance in the upper-right corner, and the Tamura-Nei model with a rate of variation among sites modelled with a gamma distribution (shape parameter = 4) in the lower-left corner. Grey = average distance within groups. Abbreviation: na = not applicable.

| | ***L. gigantea*** | ***L. medusa* 1** | ***L. medusa* 2** | ***L. davidi* sp nov. (larger)** | ***L. davidi* sp nov. (smaller)** | ***Loimia* sp. 1** | ***L. borealis*** | ***Loimia* sp. 2** | ***L. ingens*** | ***L. arbórea* 1** | ***L. bandera*** | ***L. arborea* 2** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Loimia gigantea* | 0.002 | 0.190 | 0.192 | 0.200 | 0.197 | 0.188 | 0.183 | 0.168 | 0.205 | 0.194 | 0.191 | 0.230 |
| *L. medusa* 1 | 0.230 | na | 0.184 | 0.201 | 0.204 | 0.184 | 0.204 | 0.191 | 0.176 | 0.202 | 0.191 | 0.224 |
| *L. medusa* 2 | 0.239 | 0.223 | na | 0.184 | 0.197 | 0.194 | 0.194 | 0.198 | 0.184 | 0.186 | 0.194 | 0.261 |
| *L. davidi* sp. nov. (larger) | 0.248 | 0.254 | 0.226 | na | 0.021 | 0.192 | 0.204 | 0.231 | 0.209 | 0.186 | 0.176 | 0.259 |
| *L. . davidi* sp. nov. (smaller) | 0.243 | 0.258 | 0.244 | 0.022 | 0.011 | 0.210 | 0.202 | 0.243 | 0.222 | 0.198 | 0.196 | 0.263 |
| *Loimia* sp. 1 | 0.230 | 0.224 | 0.241 | 0.238 | 0.266 | 0.003 | 0.168 | 0.187 | 0.151 | 0.199 | 0.189 | 0.222 |
| *L. borealis* | 0.224 | 0.255 | 0.236 | 0.258 | 0.254 | 0.201 | 0.000 | 0.185 | 0.198 | 0.178 | 0.194 | 0.225 |
| *Loimia* sp. 2 | 0.204 | 0.236 | 0.246 | 0.308 | 0.327 | 0.232 | 0.230 | 0.005 | 0.164 | 0.182 | 0.181 | 0.227 |
| *L. ingens* | 0.258 | 0.211 | 0.222 | 0.270 | 0.288 | 0.178 | 0.248 | 0.196 | 0.003 | 0.211 | 0.168 | 0.241 |
| *L. arborea* 1 | 0.239 | 0.249 | 0.225 | 0.228 | 0.245 | 0.249 | 0.217 | 0.222 | 0.268 | 0 | 0.152 | 0.253 |
| *L. bandera* | 0.235 | 0.236 | 0.238 | 0.213 | 0.243 | 0.234 | 0.241 | 0.221 | 0.199 | 0.183 | 0 | 0.214 |
| *L. arborea* 2 | 0.298 | 0.282 | 0.354 | 0.351 | 0.361 | 0.282 | 0.291 | 0.292 | 0.312 | 0.336 | 0.269 | na |

Sister group relationships between the Azorean clade and the rest of the sequences from other congeners are poorly supported, but there are some indications (although bootstrap values are around 60) that the sequences from a specimen identified as *L. medusa* from an unknown locality (Siddall *et al.* 2001), and the Chinese specimens of *L. arborea* Moore, 1903 and *L. bandera* Hutchings, 1990 seem to be closely related (Fig. 8).

PTP analyses group the 31 sequences of *Loimia* in eleven clusters, with those from the small and large morphotypes of our new species lumping in a single entity. The other congeners are delimited as outlined into the main clades after ML analyses. The mPTM model lumps all sequences in the large clade branching off at the base of the tree (including the largest and small specimens of our new species together with specimens identified as *L. medusa* 2 from an unknown locality, *L. arborea* 1 from the Yellow Sea and *L. bandera* from Taiwan Strait) in a single entity, a result that we interpret as an underestimation of the actual diversity of the group, given the sequence divergence (> 17%) and their disjoint geographic origins.

The identity of some of the *cox1* sequences of *Loimia* available at GenBank needs a taxonomic revision. For instance, the sequence assigned to *Loimia ingens* (Grube, 1878) from Phuket, Thai Andaman Sea (Colgan *et al.* 2001) always nests with the unidentified sequences of *Loimia* sp. 1 from the eastern (Goa, Arabian Sea) and western (Pondycherry, Bay of Bengal) coasts of India. They show an intraspecific genetic variability of 0.3% (Table 4), suggesting they belong to the same species. Conversely, the South China Sea sequences also assigned to *L. ingens* are in an independent clade to those from Thailand. Members of this clade are geographically closer to Bohol, Philippines (the type locality of the species),

but given the levels of variability we are here reporting, their identity would be reasonably confirmed only after being able to include sequences of Bohol specimens in the analysis. Moreover, *L. ingens*, also recorded along the Australian coasts, exhibits considerable morphological variation, being thus regarded as a species complex (Hutchings & Glasby 1988). Similarly, *L. arborea*, originally described from Suruga Bay (Pacific coast of Japan) (Moore 1903), shows the British Columbia (Carr *et al.* 2011) and the Yellow Sea (Wang *et al.* 2020) sequences attributed to this species as being unrelated in our tree (Fig. 8). The same occurs with two non-related specimens identified as *L. medusa* (Siddall *et al.* 2001) (Fig. 8).

### *Morphological analyses*

We have successfully reconstructed the morphospace for 28 species of *Loimia* based on twelve traditionally used taxonomical characters (Fig. 9). We observe a polarization of the morphospace space according to the body size, although this polarization is considerably reduced if body size is not included in the hypervolume calculation (Supp. file 1: Fig. S1). The descriptive metrics of richness and dispersion are smaller in the hypervolume of the larger morphotypes, somehow indicating less morphological disparity amongst those than amongst the smaller ones, while the evenness of the large species morphospace was instead larger than that of the small ones, indicating a more homogenous species distribution within the morphospace in the former. Yet, our analysis relies only on the available published data, which does not account for all intraspecific variability. Both hypervolumes show a considerable overlapping, with a value of total beta diversity of 0.92.

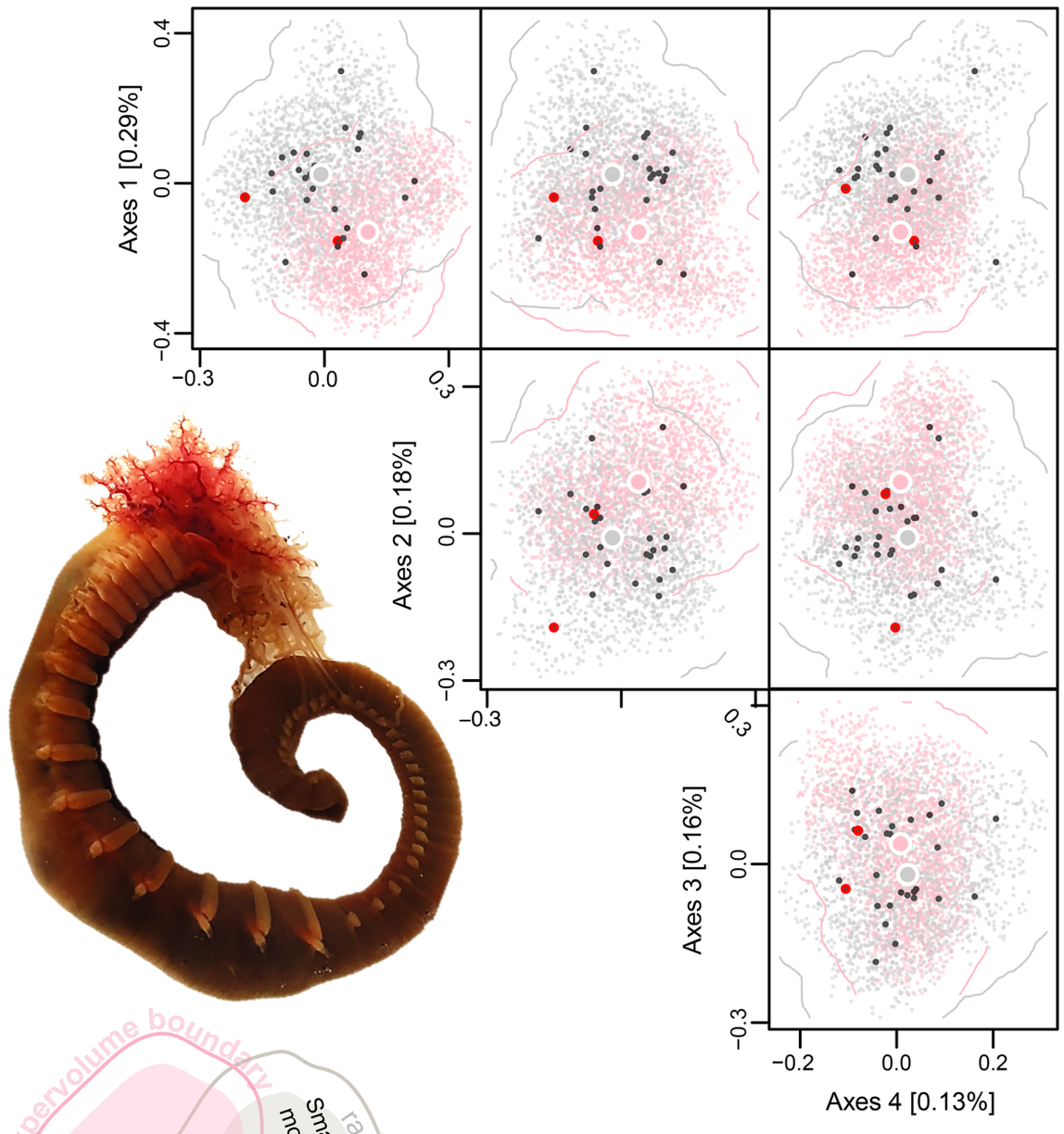
The Euclidian distance in the morphospace between the larger and smaller specimens of our new species is 0.285, well within the range of variation observed across other pairs of species of *Loimia* (i.e., 0.02–0.63). These differences are not only affected by body size but probably also by the presence of comparatively rare characters in the small individuals of our new species, such as the presence of eyespots.

## Discussion

### Short genetic distances allow reinterpreting morphological variation

The large and small morphotypes of *Loimia davidi* sp. nov. differ in several characters that are normally diagnostic for the species of *Loimia*. The short genetic distance is comparable to the intraspecific distance in other annelids (e.g., Álvarez-Campos *et al.* 2017; Sun *et al.* 2017; Nygren *et al.* 2018; Aguado *et al.* 2019) and the results of the PTP/mPTP analyses. Thus, it indicates that both morphotypes belong to a single species with size-dependent morphological variability, either related or not with sexual dimorphism. To some extent, this is comparable to other annelids having males much smaller than females (e.g., Hartman & Boss 1965; Rouse *et al.* 2004; Vortsepneva *et al.* 2008). However, despite the large specimen of *L. davidi* sp. nov. being a mature female, no gametes were seen in the small specimens. As an alternative, large and small morphotypes could represent two lineages so recently split that the morphological differences are not yet fully reflected in the genetic marker used in our analysis. Similar scenarios were described for *Mesochaetopterus xerecus* Petersen & Fanta, 1969 and *Mesochaetopterus rogeri* Martin, Gil, Carreras-Carbonell & Bhaud, 2008 (Martin *et al.* 2008) or *Ophryotrocha geryonicola* (Esmark, 1874) and *Ophryotrocha mediterranea* Martin, Abelló & Cartes, 1991 (Martin *et al.* 1991; Lattig *et al.* 2017). Indeed, the young and complex geological history of São Miguel Island, presumably affected by marine extirpation events during the Pleistocene (Ávila *et al.* 2008), provides an excellent scenario for ecological speciation events, driven by niche differentiation within this comparatively reduced geographical area and likely being associated with some degree of progenesis. However, given our data, any argument in this direction is merely speculative.

Given the nature of the observed morphological differences, we have considered both morphotypes as corresponding to different ontogenetic stages of the same species. Among terebellids, variations in




**Morphospace metrics**

| | Richness | Dispersion | Eveness |
|---|---|---|---|
| Large species | 0.0117 | 0.2825 | 0.4645 |
| Small species | 0.0231 | 0.3233 | 0.3569 |

**Fig. 9.** N-dimensional morphospace for the 28 species of *Loimia* Malmgren, 1866, calculated for the larger (body length >100 mm, grey) and smaller (body length < 100 mm, pink) species separately; red dots = larger and smaller individuals of *Loimia davidi* sp. nov.; large points with white borders = centroids of each hypervolume; hypervolume shape and boundaries defined by 5000 random points; table = summary of hypervolume richness, dispersion and evenness.

morphological characters linked to ontogeny and development have mostly been described for larval and post-larval planktonic stages. However, there are also reports of such a variation in benthic stages (i.e., from post-settled juveniles to full-grown ripe adults), which may include changes in the type, number and morphology of chaetae and uncini (Garraffoni & Lana 2010). In *Eupolymnia nebulosa* (Montagu, 1819), for example, the number of chaetal types varied from pelagic larvae to benthic individuals, while the size of uncini tripled in two years (from a two-month juvenile to a two-year adult) (Bhaud 1988; Bhaud & Grémare 1988). In *Loimia* from the English Channel, the size of juveniles increased during the post-larval development, acquiring more abdominal segments and branchial branches, but also gaining chaetae and uncini in each bundle (Wilson 1928). Our decision is thus supported by hypothesising that this process might continue in adults of other species, as the worm grows to reach the so-called gigantic size. Interestingly, the gigantic *L. gigantea* and *L. davidi* sp. nov., both reaching more than 30 cm long, are the only known species with three types of capillary chaetae. Indeed, in *L. davidi* sp. nov. the number of capillary types increases from two to three and the uncini double their length when comparing the small and large morphotypes. Therefore, our data, along with the previously existing ontogenetic evidence, indicate that both Azorean morphotypes are conspecific.

The existence of putative size-dependent morphological variability in *L. davidi* sp. nov. conflicts with the criteria previously used to diagnose species of *Loimia*. For instance, *Loimia megaoculata* Carrerette & Nogueira, 2015, from Brazil, showed conspicuously big eyespots, poorly developed branchiae, lateral lobes and ventral shields, and a colourless, slightly transparent body-wall (Carrerette & Nogueira 2015). All these characters might derive from the overall small size of the examined specimens, which could likely represent juveniles sensu Wilson (1928). In parallel, *Loimia armata* Carrerette & Nogueira, 2015, a sympatric species found in the same habitats and depths, reaches 34–40.2 mm in length and 3.2–3.5 mm in width (versus 3.7–5.1 mm long, 0.3–0.9 mm wide in *L. megaoculata*) (Carrerette & Nogueira 2015). Accordingly, it is conceivable that these two Brazilian species could represent two developmental stages of the same entity, with the specimens of *L. megaoculata* being the juveniles of *L. armata* and, the former being synonym of the latter.

**On the presence of extremely large specimens in *Loimia***

We here describe another giant species within *Loimia*. However, we agree with Lavesque *et al.* (2017) in that these do not represent cases of gigantism as defined for deep-sea organisms (Nybakken 2001; Herring 2002). The existence of these very big specimens within *Loimia* was considered something exceptional (Lavesque *et al.* 2017). Indeed, a careful examination of the existing literature has revealed the presence of at least another very big terebellid (i.e., sixteen inches long, approx. 40.5 cm). *Terebella gigantea* Montagu, 1819 (Fig. 10), originally found in shallow waters at Kingsbridge Estuary (Devon, English coasts of the western English Channel), was described as "Body long, with numerous articulations furnished the whole length with peduncles, and a few with fasciculate bristles; but the seventeen anterior joints have the fasciculi most conspicuous, being always erected, and remaining so after dead" (Montagu 1819). With these morphological attributes, the specimen described does not correspond with the present diagnosis of *Terebella* Linnaeus, 1767, which includes thoracic chaetigers on more than 25 segments, with notopodia on a variable number of segments, frequently to posterior end of body (Nogueira *et al.* 2015). Instead, it matches with the diagnostic features of *Loimia* in having 15 thoracic chaetigers in a well-defined thorax.

*Terebella gigantea* was recombined as *Loimia gigantea* by McIntosh (1922) and then transferred to *Amphitrite* Müller, 1771 by McIntosh (1922), based on specimens collected by himself at Salcombe Harbour (just at the mouth of Kingsbridge Estuary) and in France by P. Fauvel. Unfortunately, the morphology of the uncini was not described by Montagu (1819) and there is no type material for his species. In turn, the description by McIntosh (1922) showed serrated limbate chaetae instead of the smooth ones reported by Montagu (1819) for *T. gigantea*. McIntosh (1922) also synonymised *Amphitrite*

*edwardsi* Quatrefages, 1866 with *A. gigantea* based on the overall morphology, the types of limbate chaetae and the uncini. Despite providing a succinct description, Quatrefages (1866) distinguished the specimen collected in France at Saint Vaast from the British *T. gigantea* based on the number of thoracic segments and ventral shields. We certainly agree with that distinction, particularly on the basis of the colour drawing of the French *A. edwardsi*, as well as on the fact that they have different types of chaetae and uncini. Nevertheless, numerous authors followed McIntosh (1922) and reported his erroneous synonymy, including Fauvel (1909), Allen (1915), Hessle (1917), and Hartman (1959), among others. Lately, Holthe (1986) transferred *A. edwardsi* to *Neoamphitrite edwardsii* (Quatrefages, 1866). However, according to our observations, none of this material refers to a species of *Loimia*, except very likely the original *T. gigantea* of Montagu (1819). In fact, this specimen from Devon showed some key characters supporting its inclusion within *Loimia*. Among them, there are "seventeen pairs of exerted fasciculi [...] the seventeen anterior joints have the fasciculi most conspicuous, being always erected, and remaining so after death", and particularly "the first eight joints have a broad plate on the back different in structure from the rest; they are of a rufous-brown colour, shaded with purplish-black, continuing down the back in a decreasing line". As for the abdominal region, Montagu (1819) stated "beyond the seventeen first joints the peduncles are very small, and appear to be destitute of fasciculi; and they incline gradually from the sides to the back, till towards the extremity they almost meet, forming two dorsal lines" and, about the branchiae: "the three pairs of branchiae are much ramified, and red". However, the clearest clue is the drawing included in his paper (Montagu 1819: pl. xi; Fig. 7). This illustration clearly shows most of the main characteristics of the species, including the lateral lappets, the thoracic and abdominal

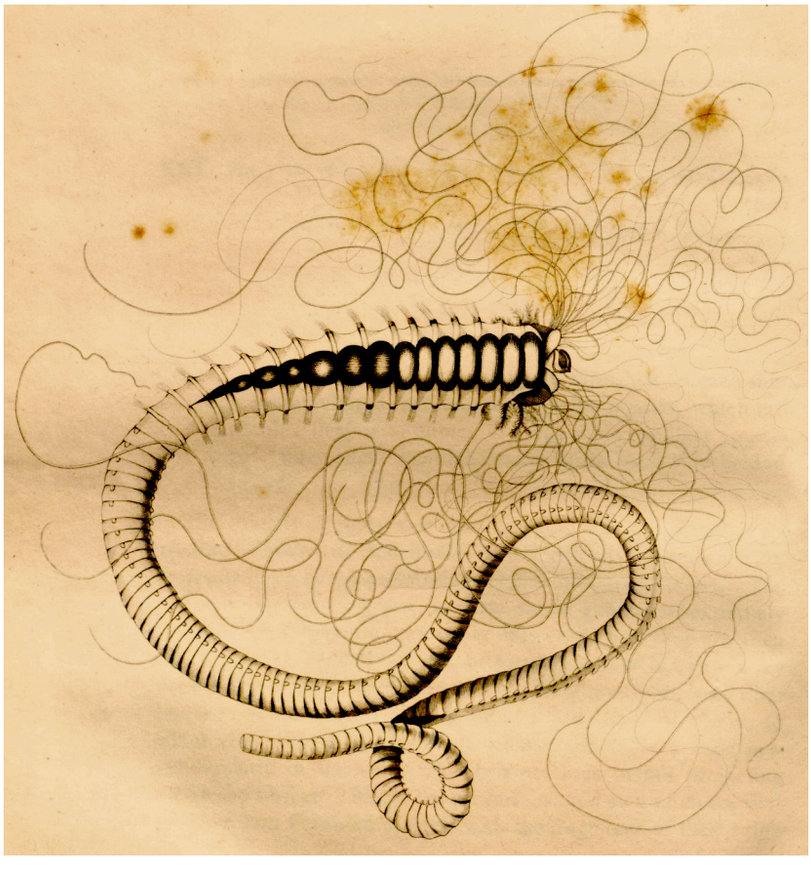


**Fig. 10.** Original drawing of *Terebella gigantea* Montagu, 1819 by Eliza Dorville, included in Montagu (1819: pl. xi) and downloaded at http://biodiversitylibrary.org/page/758907 [accessed 12 Dec. 2018].

segments, and the elongated, triangular ventral shield. This, together with the large size of the specimen, supports the presence of another giant species of *Loimia* at Kingsbridge Estuary. This location faces the sites in Brittany from where *L. ramzega* was described, being only separated by a relatively short distance across the Western English Channel. Therefore, we support the hypothesis that the English species is conspecific with that from Brittany, with the specific epithet given by Montagu (1819) and recombined by McIntosh (1922), *L. gigantea*, having priority over that by Lavesque *et al.* (2017).

The presence of a giant species of *Loimia* in the Western English Channel almost two centuries before the recent report of *L. gigantea* (as *L. ramzega*) by Lavesque *et al.* (2017) seems to contradict the hypothesis of the species being introduced in the area along with Pacific oysters intensively farmed in the area. Migration from Southern Europe or from Africa (due to climate change) and a tropicalization of the English Channel can be discarded as reasons to explain the presence of a species of *Loimia* in European waters (Lavesque *et al.* 2017). Instead, at least some of them seem to be native to NE Atlantic waters, as confirmed by the presence in the Açores of *L. davidi* sp. nov. In turn, the reasons explaining the very scarce formal reports more likely lay in the rarity of the giant specimens, as well as in relative collecting difficulty. Moreover, we cannot discard the possible misidentification of the presumably existing and likely more abundant small individuals under *Loimia* sp. or *L. medusa* from previous surveys along European coasts (Lavesque *et al.* 2017). Indeed, our findings certainly support the absence of *L. medusa* from this region.

However, care must be taken when examining the small specimens. The presence of *L. medusa* was suggested to be restricted to the surroundings of the type location in the Persian Gulf (Hutchings & Glasby 1995). Its subsequent report in the Mexican Caribbean Sea should be considered as doubtful, as the worldwide reports of the species might represent a complex of sibling species (Londoño-Mesa & Carrera-Parra 2005). Moreover, *L. minuta*, originally described from Florida (Treadwell 1929) and later synonymised with *L. medusa*, was reinstated by Londoño-Mesa & Carrera-Parra (2005) based on specimens from the Mexican Caribbean and then redescribed based on the type material by Londoño-Mesa (2009). In addition to their disjunct geographical distributions, the Mexican Caribbean and Floridian populations showed noticeable differences, particularly in the types of notochaetae and in the size of the uncini. This, together with the size-dependent morphological variation we are here reporting, reinforces the necessity of reviewing this genus worldwide, which is clearly much more diverse than currently recognised.

**Conclusions**

We describe *Loimia davidi* sp. nov. as a new species of Terebellidae (Annelida), which (1) constitutes an independently evolving entity according to the species delimitation analyses based on a cytochrome c oxidase I fragment and (2) shows a unique combination of morphological characters.

*Loimia davidi* sp. nov. shows intraspecific variability related to the overall size of individuals, with observed size-dependent morphological differences, including characters traditionally considered to be taxonomically relevant at the species level among *Loimia*. This leads us to (1) suggest reevaluating previous descriptions of sympatric new species showing similar differences in size (e.g., the Brazilian *L. megaoculata* and *L. armata*) and (2) strongly recommend taking them into account in future taxonomic studies on Terebellidae, including new species descriptions, which will undoubtedly benefit from integrative approaches combining morphological and molecular techniques.

We conclude that the type species of *Loimia*, *L. medusa* (originally described from the Gulf of Suez), is likely absent (unless introduced) from European waters, with worldwide reports certainly corresponding to a species complex. However, our data support that: (1) in addition to the Azorean *L. davidi* sp. nov., *Loimia* includes at least one European native species, its presence being known since almost two centuries ago and (2) the valid name of this species is *L. gigantea*, which we consider a senior synonym

of both *L. montagui* and *L. ramzega* and, probably, also corresponds to many of the existing records of *L. medusa* in European waters.

Although our comparative analyses are mostly limited to the available literature, we expect our results to encourage future research on *Loimia* in European and nearby waters, thereby filling the current knowledge gap between our broad understanding of the functioning of coastal ecosystems at a global scale and the details of the taxonomic and functional diversity of specific marine habitats at smaller geographical levels.

## Data availability statement

The data underlying this article are available in the published paper and in its online supplemental material.

## Acknowledgements

The authors would like to thank Nicolas Lavesque and Benoit Gouillieux for kindly sending us two specimens of *L. gigantea* (as *L. ramzega*) for morphological comparison, Mario Londoño-Mesa for kindly helping us to clarify key morphological features of some Caribbean species of *Loimia*, João Gil for his insightful comments on the manuscript, particularly on the complex ancient bibliography, and Stefano Mammola for his helpful comments on using *n*-dimensional hyperspaces. This paper is a contribution of DM to the Consolidated Research Group on Marine Benthic Ecology of the Generalitat de Catalunya (2017SGR378) and of ACC to the Operational Programme for Competitiveness Factors – COMPETE and Portuguese National Funds through FCT–Foundation for Science and Technology (grant numbers UID/BIA/50027/2019 and POCI-01-0145-FEDER-006821). MC is supported by the Ramón y Cajal program (RYC-2016- 20799) funded by Spanish MINECO, Agencia Estatal de Investigación, Comunidad Autónoma de las Islas Baleares and the European Social Fund. The authors are also thankful to the Regional Government of the Açores for having funded the Açores Workshop on Polychaete Taxonomy [grant numbers M3.3.B/ORG.R.C./076/2017, DRCT-M1.1.a/005/Funcionamento-C-/2019 (CIBIO-A)].

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*Manuscript received: 3 February 2022*
*Manuscript accepted: 26 May 2022*
*Published on: 1 August 2022*
*Topic editor: Tony Robillard*
*Desk editor: Kristiaan Hoedemakers*

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**Supp. file 1.** Additional data and figures on *Loimia davidi* sp. nov. and on the currently known species of *Loimia*. Video S1. Video recording of the living largest specimen of *Loimia davidi* sp. nov. Table S1. Character codification used in hypervolume calculations. Table S2. Character codification for the species of *Loimia* used in hypervolume calculations. Table S3. Summary of the morphological characters of all currently described species of *Loimia*. Figure S1. N-dimensional morphospace for the 28 species of *Loimia*. https://doi.org/10.5852/ejt.2022.833.1887.7469